PROCEEDINGS OF THE INTERNATIONAL CONGRESS OF PLANT SCIENCES

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Edited by B. M. DUGGAR

VOLUME II

CONTENTS, VOLUME 2

FOREWORD TO VOLUME 2

After devoting considerable time to the collection of the manuscripts representing the papers presented at the International Congress of Plant Sciences, an estimate of the probable extent of the "Proceedings" was made for the Publication Committee.[1] This estimate placed the number of printed pages at somewhat above 1400, including text figures, together with more than one hundred plates. The editor cooperated as far as possible in this survey of the situation, but it was realized that any estimate would be rather hazardous owing in large part to the diversity in size and typography of manuscript pages. The fact that many papers were hand-written added materially to the usual difficulties. Furthermore, other factors in the uncertainty arose from the unfinished nature of some of the papers, at the time, as well as from the character of the illustrations.

Besides the two addresses delivered before the Congress as a whole (by F. A. F. C. Went and Erwin F. Smith), the papers presented before seven sections were edited and submitted as Volume 1. Anticipating somewhat, as the editorial work progressed, that our estimate was low, there was a conservative restriction of text figures, an abridgment of several papers, and an elimination of the abstracts of papers so far as seemed practicable. In spite of these efforts, Volume 1 required a total of 950 pages.

There remained for Volume 2 the papers presented before six sections (Horticulture, Physiology, Pathology, Pharmacognosy and Pharmaceutical Botany, Taxonomy, and Mycology), together with the general proceedings and incidental organization features. A more careful survey of the material remaining was possible after the publication of Volume 1, and every effort was then made to conserve space and to condense where it seemed practicable to do so. Much material, including illustrations, prepared for the general proceedings was sacrificed for the scientific papers; but even with this curtailment it was necessary to omit a number of important papers submitted by persons unable to attend the Congress, the papers being listed to be read by title only. In addition the editor regrets exceedingly that two papers in later sections were not published; these omissions being purely on account of the practical necessities of cost and responsibility.

As the last pages go to press it appears that the two volumes will total about 1800 printed pages, in spite of the fact that the size of the page is somewhat larger than is employed in current American botanical journals. This reference to the volume of material included is made merely to disarm, as far as it may, any criticism of the failure to include all available scientific papers and abstracts, also the failure to add that personal touch that would have been given by in-

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[1] This committee consisted of J. R. Schramm and Lester W. Sharp of the Program Committee; George T. Moore, Treasurer; and H. H. Whetzel and B. M. Duggar (Chairman) of the Organizing Committee.

cluding with the general proceedings the group photographs of the various sections.

It should be recalled that while the Program Committee, as well as the Organizing Committee, had in mind from the beginning the publication of whatever might seem practicable in the way of proceedings, no promises of publication were made to anyone at any time in connection with the acceptance of papers for the Congress. Finally, these explanations of procedure and references to the extent of the proceedings would be incomplete if the editor omitted to acknowledge to the George Banta Publishing Company his satisfaction at their willingness to carry through this undertaking on a scale essentially inclusive of all the work of the Congress.

B. M. DUGGAR

THE APPLE IN CANADA, WITH ESPECIAL REFERENCE TO THE SOURCE OF ORIGIN OF RECOMMENDED VARIETIES AND THE BREEDING OF NEW ONES[1]

W. T. MACOUN

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The apple industry has become a very important one in the Dominion of Canada. Great areas there are suited to the production of apples. The chief and most extensive commerical orchards are situated in certain parts of the Provinces of Ontario, Nova Scotia, Quebec, and British Columbia. Apples can, however, be grown in every province of the Dominion, though, at present, in the Prairie Provinces of Manitoba, Saskatchewan, and Alberta, it is only under the most favorable conditions, although the hybrid crab apples may be grown in these provinces in abundance over a very wide territory and under very trying conditions.

NUMBER OF APPLE TREES IN CANADA—CENSUS OF 1921

The following figures in Table 1, from the Census of 1921, the latest available, will give some idea of the number of apple trees in Canada.

TABLE 1. DISTRIBUTION OF APPLE TREES IN THE VARIOUS PROVINCES

Province	Bearing	Non-bearing
British Columbia	1,625,696	515,821
Alberta	14	259
Saskatchewan	26	204
Manitoba	703	2,542
Ontario	4,492,672	987,115
Quebec	779,394	556,899
Prince Edward Island	132,678	22,162
New Brunswick	397,338	145,358
Nova Scotia	1,822,396	294,049
Total	9,250,917	2,524,409

In Table 2 will be found the estimated number of barrels produced in Canada for the 5 years 1921–25 with average value per barrel.

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[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 17, 1926.

TABLE 2. COMMERCIAL APPLE PRODUCUION IN CANADA 1921-1925

		Barrels	Value	Average value per barrel
Canada	1921	5,367,700	$35,821,090	$6.67
	1922	5,048,405	24,692,182	4.90
	1923	4,493,183	24,489,350	5.45
	1924	3,375,084	19,747,772	5.85
	1925	3,580,770	20,057,417	5.60
Nova Scotia	1921	2,036,065	11,096,554	5.45
	1922	1,891,852	7,851,185	4.15
	1923	1,821,064	8,012,682	4.40
	1924	1,274,742	6,118,761	4.80
	1925	956,056	4,302,252	4.50
New Brunswick	1921	138,589	692,945	5.00
	1922	173,236	779,562	4.50
	1923	69,292	329,137	4.75
	1924	86,615	454,728	5.25
	1925	69,292	367,247	5.30
Quebec	1921	124,564	704,686	5.66
	1922	216,984	1,518,888	7.00
	1923	65,094	488,205	7.50
	1924	109,500	766,500	7.00
	1925	109,004	741,227	6.80
Ontario	1921	1,932,280	13,719,188	7.10
	1922	1,739,000	7,608,050	4.37
	1923	1,304,400	6,717,660	5.15
	1924	913,080	4,884,978	5.35
	1925	1,587,848	8,336,202	5.25
British Columbia	1921	1,136,202	9,607,717	8.46
	1922	1,027,333	6,934,497	6.75
	1923	1,233,333	8,941,666	7.25
	1924	991,147	7,522,805	7.59
	1925	858,570	6,310,489	7.35

VARIETIES OF APPLES RECOMMENDED FOR COMMERCIAL PLANTING IN CANADA

A very large number of varieties of apples, originating in the principal apple producing countries of the world, have been tested in Canada. The following list of 40 varieties recommended for commerical planting there is based on the experience of many ochardists throughout Canada and on experiments conducted at federal and provincial institutions in the Dominion:

Summer	Degree of hardiness	Origin
Astrachan	3	Russia
Blushed Calville	1	Russia
Charlamoff	1	Russia
Crimson Beauty	2	Canada (New Brunswick-Russian parentage)
Duchess of Oldenburg	1	Russia
Lowland	2	Russia
Melba	3	Canada (Ontario)
Transparent	2	Russia

Autumn	Degree of hardiness	Origin
Alexander	3	Russia
Anis	1	Russia
Antonovka	1	Russia
Blenheim	4	England
Dudley	2	United States (Maine-Russian parentage)
Gravenstein	5	Germany
Hibernal	1	Russia
Lobo	3	Canada (Ontario)
McMahan	2	United States (Wisconsin-Russian parentage)
Okabena	2	United States (Minnesota-Russian parentage)
Ostrakoff	1	Russia
Patten Greening	1	United States (Iowa-Russian parentage)
Wealthy	2	United States (Maine-Minnesota-Russian parentage)

Winter		
American Golden Russet	3	United States (Massachusetts)
Baldwin	5	United States (Massachusetts)
Bethel	3	United States (Vermont)
Cox Orange	4	England
Delicious	4	United States (Iowa)
Fameuse	3	Canada (Quebec)
Gano	4	United States (probably Kentucky)
Grimes	4	United States (West Virginia)
Hubbardston	4	United States (Massachusetts)
Jonathan	5	United States (New York)
McIntosh	3	Canada (Ontario)
Northern Spy	4	United States (New York)
Rome	4	United States (Ohio)
Rhode Island Greening	5	United States (Rhode Island)
Ribston	4	England
Scott Winter	3	United States (Vermont)
Stayman	4	United States (Kansas)
Tompkins King	4	United States (New York)
Tolman	4	United States (probably Massachusetts)
Wagener	5	United States (New York)
Winesap	5	Origin unknown

It will be noticed that 6 of the 8 summer varieties are of Russian origin and 1 of the remaining 2 is of Russian parentage. Of the 11 autumn sorts, 3 are of Russian origin, and 5 of the remaining 6 of Russian parentage, the Gravenstein being the only 1 of the 11 not of Russian parentage. It is significant that this variety is useful in only the milder parts of the commerical apple districts. Of the 21 winter varieties, not one is of Russian parentage so far as is known. It may be said, however, that in some parts of Canada, where the growing season is relatively cool, varieties that are called summer and autumn in the above list become autumn and winter there. The seasons given in the table are for those parts of Canada where most of the apples are grown.

We shall now analyse the information available in regard to some of the varieties recommended for planting in the Dominion beginning with a short history of the introduction of the apple into Canada.

When that part of North America, which is now called Canada, was first settled by white men in the early part of the 17th century, the settlers brought with them from Great Britian and Europe apple seeds and young apple trees.

The parts of Canada which were settled first were what are now called the Provinces of Nova Scotia and Quebec. It was in the milder parts of Nova Scotia where the early French settlers established themselves, and, while the winters were somewhat colder than in France, it was possible to grow almost any variety or seedling of any variety of apple from that country, and, when the English took possession later on they found that the English varieties succeeded well. Quite the opposite was the case, however, when varieties either from France or Great Britain were tried along the St. Lawrence River, in what is now the Province of Quebec, where winters are much more severe. It was only in rare instances that trees succeeded. The origin of that well-known variety, the Fameuse, which has made Quebec famous, so far as the apple is concerned, and has yet scarcely a rival in the fine character of its flesh and delicate flavor, is one of the very few old varieties that would seem to be of French origin, or from a seedling of a French variety. It has been known in Canada since the 18th century, but its origin has not yet been established, although Canada claims it. While the Fameuse is hardy enough for the milder parts of the Province of Quebec and will withstand an occasional drop to −30°F., it is not one of the hardiest varieties, and, from time to time, many trees are winter-killed, the last loss occurring after the winter of 1917–18. There has been a number of open pollinated seedlings of this variety named, from time to time, during the past One Hundred years either in Canada or the United States, and, although the records are rather uncertain, those which are supposed to be seedlings of the Fameuse are: Shiawassee, St. Lawrence, Scarlet Pippin, Louise, and McIntosh. All of these originated in Canada except the Shiawassee. None of these appear hardier than Fameuse, if as hardy, except the McIntosh, which is distinctly hardier. The McIntosh was found with some other seedlings near his home by John McIntosh, Dundela, Matilda Township, Dundas Co., Ont., in 1796, and has proven to be the most valuable variety to Canada of any variety originated there or in any other country. It has become one of the most important apples in the United States. It is supposed to be a seedling of Fameuse, but none of the many seedlings raised from it resemble Fameuse to any marked extent while many resembel the McIntosh itself in several marked characters.

Another of the apples which has proved of great value in Canada is the Wealthy. This originated with Peter Gideon, Excelsior, Minnesota, about 1860, and he stated when it was introduced about 1869 that it was grown from seed of crab apples grown in the State of Maine. Open pollinated seedlings from this apple have not shown crab apple characters to any marked extend, there being only 2.57 per cent of seedlings raised at Ottawa having small crab-like fruit. However, the crab blood in it, if Gideon's statement is correct, has, doubtless, given it the hardiness which has helped to make it one of the most important apples in Canada.

The Duchess of Oldenburg is another very valuable apple in Canada. It is generally considered of Russian origin, and is certainly one of the hardiest varieties grown in the Dominion.

Yellow Transparent is another Russian sort which is very generally planted in a limited way as it is one of the earliest summer apples.

Thus, of these 5 varieties of apples now recommended for planting in Canada, Fameuse and McIntosh are of Canadian origin; Wealthy of Vermont-Minnesota origin; while Yellow Transparent and Duchess of Oldenburg are Russian varieties. These are the 5 varieties recommended for commerical planting in the colder, though not the coldest parts of Canada, where apples are grown commercially.

THE RUSSIAN APPLE IN CANADA

The small list of varieties of apples suitable for planting in any but the most favored parts of Canada from a climatic standpoint was recognized many years ago when it was realized that other varieties which had survived the climatic conditions in countries as cold as Canada must be obtained and new varieties originated in Canada itself, and, as Russia was the outstanding country with cold climates where apples had been in cultivation for a long time, it was from that country that it was hoped would come more good varieties suitable for growing in the colder parts of Canada, and a brief history of their introduction and dissemination in America, and especially in Canada, may be given here.

Russian varieties have played an important part in the development of apple culture in Canada both for what they have done to help the commerical side of the industry and for the reason that they have enabled people living in the colder parts of Canada to grow apples for their own use. The varieties which are now widely planted commercially in the Dominion are: Duchess of Oldenburg, Yellow Transparent, and, to a less extent, Red Astrachan, and Alexander. By far the most important is the Duchess of Oldenburg.

It was early in the 19th century that the Russian apples were introduced into the United States, and they soon found their way into Canada, where their hardiness and suitablity for the colder parts of the Dominion made them popular. Comparatively few Russian varieties, however, were grown until the United States Department of Agriculture introduced a large number of varieties in 1870, and distributed them to various places in the United States. But few trees of this shipment came to Canada at that time. There were 202 varieties in this shipment which were considered distinct, though the nomenclature was very much confused. The Iowa Agricultural College, Ames, Iowa, through the Professor of Horticulture, J. L. Budd, made several importations, one of 72 varieties in 1879. These were procured through Dr. Regel, then Director of the Imperial Botanic Gardens, St. Petersburg, and from these and through large importations made after a visit of Prof. Budd and Mr. Chas. Gibb, Abbotsford, P. Q., Canada, in 1882, to Russia, Poland, Germany, and Austria, Canada received many varieties of Russian origin, among which there proved to be quite a number much hardier than Alexander, Red Astrachan, and Yellow Transparent, varieties which were being grown in Northeastern Russia throughout districts of the Volga and the Government of Kazan as far north as latitude 55° and where it was said the winter temperatures fell to −50°F. and below. These were much colder conditions than these apples had to endure in those

parts of Canada they were intended for at the time of their introduction. It
may be said here that few of these apples have proved valuable where they were
mainly intended for, but are playing an important part in colder districts and
in the breeding of new varieties. The largest collection of Russian apples in
Canada was established at the Central Experimental Farm, Ottawa, Ont., and,
with the importations of Budd and Gibb, and later ones obtained direct from
Russia, there were at one time 160 varieties, and at the present date 75. At
Ottawa the temperature in some years falls to $-30°$F., and at longer intervals
to $-33°$F., but in most years the lowest winter temperatures are between
$-20°$ and $-30°$F. Of the importations of Budd and Gibb, the varieties which
have proved most useful, as being exceptionally hardy, are those which are
usually called in Canada: Hibernal, Charlamoff, Anis, Antonovka, Blushed
Calville, Ostrakoff, Anisette, Duchess of Oldenburg.

It was thought by the introducers of these Russian apples that some of them
would prove valuable winter varieties, but in those parts of Canada where they
were tested in the hope that this would be the case, not a single, useful, late-
keeping sort was found. Varieties said to keep well in Russia were found to be
but autumn, or, at best, early winter varieties in the Provinces of Ontario and
Quebec, where they were most tried at first and where there must be warmer
weather than where these grow and keep well in Russia.

Apart from the great hardiness of many of the Russian varieties, most of
them have been disappointing. In quality of fruit, coarseness of flesh, great
acidity, lack of agreeable and high flavor are characteristics of many of them,
and fire blight plays havoc with the trees of quite a number. They are, on the
whole, productive, and it must be remembered that some of those longest in-
troduced are still much planted because there are few better varieties of their
season to take their place. I refer to Duchess of Oldenburg, Red Astrachan, and
Yellow Transparent particularly.

The Dominion Experimental Stations were established in 1887, and these
offered a means through which work might be begun in obtaining new varieties
suitable for Canadian conditions by systematic breeding. Some work had, how-
ever, been done previous to this time by private individuals, among whom may
be mentioned the late Chas. Arnold, Paris, Ontario, who originated the Ontario
apple; the late P. C. Dempsey, Albury, Ontario, who originated the Trenton
apple; and the late Francis Peabody Sharp, Woodstock, New Brunswick, who
originated the New Brunswick and Crimson Beauty apples. These are all still
in cultivation. Of these, the Crimson Beauty is the earliest red apple known
to us, and is hardy, but the quality is very inferior. It has been used as a parent
in crossing in the hope of obtaining extra early varieties of high color of better
quality.

As the Russian apples were still considered the most promising material to
work with in the endeavor to obtain hardier and better sorts suited to the
colder climates of Canada, seed was imported from Northern Russia in 1890 by
the Central Experimental Farm, Ottawa, and some 3000 trees grown from it.
Most of these fruited, and a few of the best were named, but only one of these,

named Rupert, is proving promising. It is a greenish yellow apple, a little earlier in season than Yellow Transparent but better in quality, and is suggestive of Early Harvest in flavor.

The chief defect in these apples of purely Russian parentage was found to be absence of high, pleasant flavor and absence of fine grained, tender flesh, just as had been the experience with the named varieties which had been introduced from Russia. None of the seedlings raised in Canada from seed from Russia and none of the imported named varieties from Russia have been found hardy enough for the higher altitudes and treeless parts of the Canadian prairies, although such Russian varieties as are known in Canada as Duchess of Oldenburg, Charlamoff, Ostrakoff, Hibernal, Blushed Calville, Beautiful Arcade, Anis, and Antonovka will, with more or less protection, fruit up to altitudes of nearly 3,000 feet, and where temperatures fall to between −40° and −50°F. in most winters, though the success with some of them is confined to the lower elevations.

ORIGINATION OF HARDIER APPLES THAN THE NAMED RUSSIAN VARIETIES

Still hardier varieties were needed for the Canadian prairies, and, when this was realized, work was begun in 1894 to obtain such kinds. Seeds of the Siberian Crab, *Pyrus baccata*, had been obtained from the Royal Botanic Gardens, St. Petersburg, in 1887, and trees grown from these had proved quite hardy in exposed places on the prairies, and it may be said here that trees from this lot of seed are still living and bearing heavy crops at Indian Head, Saskatchewan, now nearly 40 years old, and have always been hardy. In 1894, therefore, the *Pyrus baccata* was crossed with a number of the named Russian varieties and with some varieties of American origin. Some 800 trees were obtained as a result of this work, and these soon began to fruit, but none of them bore fruit larger than $1\frac{1}{2}$ inches in diameter, and most of them had the hard, breaking flesh of the crab apple. The best of these were propagated, named, and sent out to a large number of settlers in the prairie provinces of Canada, and were tested on the Dominion Experimental Farms as well. Most of those which were distributed in this way proved hardier than the named Russian apples or hybrid crab apples in commerce and were a means of giving the settlers an abundance of crab apples from which they could make jelly. Some of those which have become best established in the prairie provinces of Canada are: Osman, Columbia, Mecca, Jewel, Pioneer, Prince, Tony, Elsa, and Silvia; but, of these, there are but 2 which may be called ironclad, or which will succeed under almost any climatic condition on the prairies, and are decidedly hardier than any other cultivated varieties of apples or crab apples that have been tested in Canada.

The original brief descriptions which were made of these crab apples are here included.

Columbia (*Pyrus baccata* × Broad Green).—Tree, a very strong grower and a fair bearer. Fruit, size, 1.8 inches across and 1.6 inches deep; nearly conical, distinctly ribbed. Calyx protruding and persistent. Stem. of medium length. Color, red, with stripes and dots of a deeper shade. Flesh, yellowish, lightly streaked with red, juicy, subacid, with a pleasant flavor; slightly astringent. Quality, fair to good. Season, late September and October. Thus far free from blight.

Osman (*Pyrus baccata*×Osimoe) (The Osimoe is also known in Canada as Beautiful Arcade, Repka Kislaga, and Good Peasant).—Tree, a fair grower and a good bearer. Fruit, above medium size; a little smaller than Transcendent. Color, pale yellow well washed with crimson. Flesh, tender, breaking. Flavor, acid but pleasant, only slightly astringent. Season, latter half of August.

Second Crosses to Obtain Hardy Varieties of Apples

It will be seen that the crab apples are not large.

When it was learned that none of the first generation crosses were larger than $1\frac{1}{2}$ inches in diameter, seed was sown of some of the best of them in the hope of obtaining larger fruit in the F_2, but no larger fruit was obtained, and the great majority of the trees bore fruit smaller than the F_1.

In 1904, the best of the F_1 were re-crossed with a number of varieties of apples of Russian and American origin. Many trees from these crosses bore fruit, and fruit was obtained as large as $2\frac{1}{2}$ inches in diameter and of distinctly better quality than the F_1. The best of these were named, and are now being tested in the prairie provinces, but so far none of them appear to be as hardy as the Columbia and Osman of the F_1. Some of the best of these second crosses are: Rosilda, Piotosh, Printosh, Redman, Trail, Wapella, Angus.

Latest Crosses to Obtain Very Hardy Varieties of Apples

When the last mentioned crosses were made, the Osman and Columbia were not known to be of outstanding hardiness, and they were not used as parents, but, during the past 5 years, since this was known, they have been crossed with other varieties of apples, and in these crosses lies our present greatest hope in obtaining apples of at least $2\frac{1}{2}$ inches in diameter and hardy enough to withstand any climatic condition in Canada where there is settlement. Although it may be found that among seedlings of Russian apples now being raised in large numbers in the prairie provinces where the tenderer trees are quickly eliminated, there will be varieties hardier than any of the named Russian sorts so far tested, and some promising ones, which have already fruited, are being tested in trying situations.

New and Better Varieties for Parts of Canada Where the Apple is Grown Commercially

Most of the apple orchards in Canada are in the Provinces of Ontario, Quebec, Nova Scotia, and British Columbia, though apples are grown to a limited extent commercially in New Brunswick and Prince Edward Island and to a very limited extent in Southern Manitoba.

There is great need for better varieties as none of those grown are by any means perfect, and new sorts are wanted to cover the season better. There is great need of better summer, autumn, and winter varieties in all districts.

The Central Experimental Farm, Ottawa, Ontario, is situated in Eastern Ontario in latitude 45°. The winter climate is too cold to grow varieties such as Baldwin, Tompkins King, Northern Spy, Jonathan, or Yellow Newtown. The

varieties usually recommended for planting are: Yellow Transparent, Duchess of Oldenburg, Wealthy, Fameuse, and McIntosh. Since 1895 the endeavor has been made here to obtain other varieties which would augment this list or replace some of the varieties on it. From thousands of trees which have fruited from open pollinated and from controlled crosses, more than 100 have been considered sufficiently promising to name and send out for trial in parts of Canada where they were thought likely to prove of value. It is the policy of the Central Experimental Farm to obtain the judgment of unbiased experimenters who have tested the varieties before introducing them to the trade, and so far only 2 have been really introduced. These are called Melba and Lobo. Both are open pollinated seedlings of McIntosh, the Melba being of the season of Duchess of Oldenburg and the Lobo coming between Wealthy and McIntosh. Both are of the McIntosh type and good in quality. Other very promising apples of McIntosh or Fameuse type are: Joyce, season early September; Pedro, season September; Hume, season September; Patricia, season October; Lawfam, season December to February; Linda, season December to March. Many others might be mentioned of other types, but apples of the McIntosh type are of especial interest and value in America.

It has been the aim in the work of the Horticultural Division at the Central Experimental Farm to make as many combinations as possible rather than to have large numbers of few varieties, though that would be done also if more land were available as the McIntosh, for instance, has been found an outstanding valuable parent. It is interesting to note here that, in the crab apples referred to, when McIntosh was used as a parent, it left its impress in a marked way, giving the crosses high color and good flavor.

So far 243 combinations, including 57 varieties, have been used in this work, and it is believed that as a result of this and the work of other institutions, the list of varieties recommended for planting in Canada will undergo a great change.

In Canada there are 25 experimental stations controlled by the federal government, at most of which breeding work with apples is under way. In British Columbia more firm-fleshed, good shipping varieties are desired, and at the Summerland Station crosses between Yellow Newtown and other varieties have been made. At Morden, Manitoba, a special effort is being made to obtain hardy varieties for the Prairie Provinces, and much breeding work is being done with the hardiest varieties of apples and crab apples. At Kentville, Nova Scotia, crisp-fleshed, high-flavored varieties which will be acceptable in the British market are hoped for.

Provincial institutions, such as The Horticultural Experiment Station, Vineland, Ontario, and the Agricultural Colleges at Guelph, Ontario, Truro, Nova Scotia, Winnipeg, Manitoba, and Saskatoon, Saskatchewan, are all breeding varieties for special purposes, and with the new varieties originated by private individuals, the time should not be distant when there will be apples of Canadian origin of the highest quality for all seasons for all parts of Canada and available for planters beyond the boundaries of the Dominion.

SHALL WE TAME THE NATIVE FRUITS OR RELY UPON IMPORTATIONS?[1]

N. E. HANSEN

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The history of the world's horticulture indicates that Nature's distribution of plants was not complete, also that the Ice Age destroyed or retarded the migration of plants through natural causes. Hence, the true answer to this question is that we must improve the native species whenever possible, and when there are no native species that meet the need, importations must be made. To rely wholly upon the development of native species would sadly reduce our present fruit lists. Our American pomology is based largely upon importations. It is, no doubt, true that our native species would have received much greater attention if importations had been impossible. Hundreds of millions of dollars have been lost in America by planting fruits from milder climates of the world. The accumulated evidence goes to show that a species of plant cannot be acclimated to any extent to a greater degree of cold. By selection we may shake the sieve thoroughly, but there is left in the sieve only what was there in the first place. This variation in hardiness points to a slow process of acclimation by nature. De Candolle writes in "The Origin of Cultivated Plants": "The northern limits of wild species . . . have not changed within historic times, although the seeds are carried frequently and continually to the north of each limit. Periods of more than four or five thousand years, or changements of form and duration, are needed apparently to produce a modification in a plant which will allow it to support a greater degree of cold." We should take full advantage of this great work done for us by nature in acclimating plants, and cultivate our local form of the native species instead of the form adapted in the course of thousands of years to a mild, moist climate.

All my experience so far indicates the general truth of the idea that a plant cannot be modified to endure a greater degree of cold by selection alone. Hardiness is a gene that can be transmitted in hybridization. Acclimatization, the work of man, is impossible. Acclimation, the work of Nature, has been done long ago. Any species of plant extending over a wide area has been modified greatly in its power to resist cold.

Nurserymen have found by costly experience that many species of trees vary in hardiness. The box elder (*Acer negundo*) from the South and East winter-kills in the North, while the local northern box elder is perfectly hardy. In Russia

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[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 17, 1926.

the box elder from St. Louis, Missouri winter-killed, while the same species from Manitoba proved perfectly hardy. At the North, the red cedar from the South is tender, while the local northern form is hardy.

Much more evidence might be given along the same line, all going to show that Nature has done this work of acclimatizing species, but that thousands of years are needed for the work. The converse of the law appears to be true, that a species cannot be extended with success southward to any great extent beyond its natural limits. Usually such plants suffer from starting into premature growth during mild weather in winter.

In our discussion of hardiness we should leave out annual plants. Annual plants such as corn have been carried many hundreds of miles north of their original limits. By selection for short season the corn plant has been reduced in stature from 20 feet to 3 feet and in a season from 7 months to 3 months. Furthermore, over winter it is not a plant but a seed. The real truth of this matter is that we should obtain hardiness from plants that are hardy in the first place. For South Dakota I have found that best results come from the native species of the prairie Northwest or from similar climates of Eurasia, especially Siberia, East Russia, Mongolia, and North China. A study of isothermal lines running around the world and the study of maximum and minimum temperatures, and annual rainfall all will help to form a judgment as to where hardiness against winter cold and summer heat may be expected in the plants from any region. Ecological consideration must also be considered. Dry climates favored xerophytic plants. Large size and high quality of fruit are usually obtained best from plants that have been under cultivation for a long time. In fruits it seems that Nature provides for bright color, edible quality, and large size, mainly as a means of attracting animals that will eat the fruit and thus distribute the seeds. Man must step in to increase these qualities up to the market standard. The larger and better the fruit, the greater the value for the market. While we may obtain perfect hardiness from the native fruits, the element of time and convenience must come in, so we have relied largely upon importations. In doing this we have sadly neglected a number of choice fruits. It appears we have improved the native fruits only when it became a necessity because imported fruits failed. The American grape and American raspberry are good examples. With the new light in heredity we now know that choice quality in fruits may be regarded as a gene which can be combined with winter hardiness, also a gene, in the same plant, although the two genes come from far distant lands. This international view of fruit-breeding is the best view. Present market conditions demand the very best. To bring to market an inferior product when a better and choicer product could be grown just as well is to invite financial failure for the fruit grower. Another point to be noted is that of late years the demand for long distance transportation has brought out varieties with hard flesh and capacity for distant shipping, at the expense often of tenderness and high quality. But to carry this to excess only invites failure. If the purchaser finds that a certain fruit deteriorates in quality, he does not know just what has happened but he gives sufficient answer by turning his attention to other fruits. If we make apples taste more like potatoes the purchaser may buy other fruits the next time.

Breeding Better Apples

De Candolle considers the apple[2] to have existed in Europe, both wild and cultivated, from prehistoric times. The lack of communication with Asia before the Aryan invasion makes it probable that the tree was indigenous in Europe as in Anatolia, south of the Caucasus, and Northern Russia, and that its cultivation began early everywhere.

According to A. C. Koch[3] it is the descendant of six different species, native of the temperate parts of Europe and Asia. This process of amalgamation has taken place during the past 4,000 years. Koch found the pollen of all cultivated apples non-uniform, due to this mixed ancestry, while that of primitive species was uniform. Fixity of type, as indicated by uniformity of pollen, shows a homozygous condition.

To cross cultivated apples with each other is breeding mongrels to mongrels, because the cultivated apple is in heterozygous condition. It must be admitted that Nature with the aid of insects has been doing this work with success for thousands of years. Most of the standard varieties now in cultivation are the result of this haphazard work. Meanwhile, it is very evident that we have neglected the indigenous apples, although they have many good points. Much work has been done in amalgamating the Siberian crabapple with the cultivated apple. I have been working especially with hybrids of the indigenous American apples for many years and have obtained some interesting results. I am preparing a bulletin covering this work. It is time that our indigenous apples and the apples of Siberia receive more attention than they have received in the past.

Breeding Pears Immune to Blight

Since the pear is not native to North America, all of our pears are imported. The cultivated pear, *Pyrus communis*, is indigenous to temperate Europe and western Asia. The pear is not native of North America. The limiting factor to successful pear culture in the Northwest is fire blight (*Bacillus amylovorus*), and winter-killing. Fire blight is native of the northeastern United States, and *Pyrus communis* has not had occasion in its early history to build up any resistance to fire blight. For this we must look to the pears of northeastern Asia, especially *P. sinensis* and allied species, such as *P. calleryana* from southern China and P. *ussuriensis* from Northern China and eastern Siberia.

In 1924, on my sixth tour to foreign lands in search of new seeds and plants, I went from Seattle to Japan and through Japan to Korea, crossing southern Manchuria via Mukden, and north to Harbin on the Siberian Railway where I made my headquarters. From Harbin I went east and west on the Chinese Eastern Railway which forms a part of the Siberian line for nearly a thousand miles. I found the western limit of the pear a few miles east of Harbin. I went from village to village in the mountains and got the Chinese to bring in the pears as they ripened. The main work was in the region about fifty miles

[2] Origin of Cultivated Plants, p. 236.
[3] Pflanzen-Mischlinge (Wilhelm Olbers Focke) Berlin, 1881, p. 144.

east of Harbin. The Chinese cut down other timber in the mountains but leave the pear trees, as they furnish an annual supply of food. From many thousand pounds of pears I picked the best for special selection work. Sixty-eight pounds of seed was obtained from the fresh fruit. I hope that these pears will be carried through several generations, as was done by Van Mons in Belgium, but utilizing the latest improvements in theory and technique.

I have several hybrids coming on between these hardy Oriental pears and pears of choice quality of Europe. I think it is quite possible to obtain varieties with the choice quality of the best pears of western Europe and the hardiness and blight-resistance of tree of North Manchurian and east Siberian wild pears.

IMPROVEMENT OF THE PLUMS

"The battle of the plums," mentioned by Dr. L. H. Bailey[4] in 1895 is still being waged. The European plum proves of no value for the prairie Northwest owing to lack of hardiness. Progress has been made with seedlings of the native plum (*Prunus americana*), and also the native plum of Manitoba, *P. nigra*. Fully ten thousand seedlings of *P. americana* have been grown at this Station in the endeavor to improve the fruit in size and quality. But I found it very difficult to get any one to plant these native plums after my new hybrids with Japanese plums came on. My Waneta bears fruit two inches in diameter, weighs two ounces, and is of choice quality. The trees in the nursery are extremely vigorous, showing the hybrid vigor. This saves a year's time in nursery propagation. So far no successful hybrids have been made of native plums and European plums.

IMPROVEMENT OF THE CHERRY

The sweet cherries of Europe, so extensively raised in our eastern states and on the Pacific Coast, are not hardy in the prairie Northwest. The sour cherries of Europe are much hardier but not sufficiently hardy to recommend for general planting in South Dakota. The Early Richmond and allied varieties are grown to a small extent in the extreme southern part of the state.

At this writing the chief limiting factor in hardy cherries at the North is the tender Mahaleb and Mazzard stocks used in commercial propagation. Chief among the objections to the northern Pincherry (*P. pennsylvanica*) as a commercial cherry stock are the numerous root-sprouts. This suckering habit makes it difficult to control. The Moscow probably will not be hardy as far north as the sand cherry hybrids. But even if none of the true cherries prove sufficiently hardy at the North, some very good quality substitutes can be found among the numerous sand cherry hybrids already originated.

SAND CHERRIES

The native sand cherry (*P. Besseyi*) of Western South Dakota, is a low bush, bearing black fruit. It is one of the most important native fruits. Many thousand seedlings were fruited by the writer through several generations with the result

[4] The Survival of the Unlike, p. 418, 1895.

that the best seedlings bear fruit one inch in diameter and of good quality. The stature of the plant, however, has not been materially changed. But I have produced many successful hybrids of sand cherries with Japanese plums. Two of the best are Opata and Sapa which are extensively propagated and are very popular over a wide area, from Oklahoma north into Canada. They bear well on one year shoots in the nursery. When transplanted they bear abundantly the year after planting.

It appears to me that the future cherries for the prairie Northwest will not be cherries at all, although they will look and taste like cherries. They will be derived from some amalgamation of the sand cherries of South Dakota and the best plums of Japan.

CHOKE CHERRIES

P. virginiana and the allied species are extremely productive. I have been working with them for many years in endeavoring to improve the fruit in size and quality. It is very difficult to get the "choke" out of the fruit. However, some success has been attained in locating trees growing wild that have very little of this acerbity. This work is greatly accelerated by my discovery that the chokecherry makes a strong nursery tree budded on the May Day Tree of Eastern Siberia, *Prunus padus commutata*.

Some yellow fruited chokecherries have also been located. Prairie settlers find good use for the fruit, in its present form, for jellies, especially when mixed with apple juice.

It appears then that while the sand cherries of Europe will not acclimate to our western prairies, yet we can develop very acceptable substitutes for them from the native species.

Developing Hardy Grapes

The grape of history, *Vitis vinifera*, according to De Candolle grows wild in the temperate regions of Western Asia, Southern Europe, and Northern Africa, and has been under cultivation for many thousand years. In Egypt, the records of grape cultivation go back some six thousand years. In 1897 and 1909 while traveling through the Transcaucasus, I learned that this species is abundant in a wild state and is considered truly indigenous.

It cost America many thousands of dollars to learn that this species was not a good foundation for grape culture in the eastern part of the United States. It was not until amalgamation took place with native species of eastern America that success became possible. The grape culture of California is founded upon *V. vinifera*.

The Concord grape first fruited in 1849 and was grown from seed of the wild Fox grape, *V. Labrusca*, by E. W. Bull of Concord, Massachusetts, near the famous bridge still standing from the American Revolution.

The vine is marked by a permanent tablet. It seems eminently fitting that this "mother" vine is so honored when we reflect that 75 per cent of all the grapes raised in eastern America come from this famous Concord vine and its pure-breds

and cross-breds. But the Concord grape and its offspring, great as they are, will not help South Dakota and the prairie Northwest since even with careful winter protection they are not sufficiently hardy.

For many years past I have worked on this problem and have grown a lot of seedlings of the wild grape of the Dakotas, but this was very slow work as this wild grape is not equal to the wild Fox grape of Massachusetts in size in its original condition. So I began crossing the wild grape of the Dakotas with some of the choice tame grapes. This was done in the Fruit-breeding Greenhouse of South Dakota State College. The work was a success. In 1895 I introduced 32 of these hybrids. All are hardy at Brookings without winter protection of any kind.

In recent years, I have endeavored to trace this native grape, *V. riparia* or *V. vulpina*, to its northern and northwestern limit in Manitoba. These are now receiving attention. Hybridization is evidently the quickest way.

I have produced several thousand seedlings of wild grapes, but find them to be very fixed as to size of fruit. This line of effort should not be neglected, although it may take several generations to complete the task. By that time we will know whether hybridization of foreign species or development of the pure wild grapes by seedling selection, is the better way.

Breeding of Hardy Raspberries

The red raspberry of Europe did not prove sufficiently hardy for general cultivation in our eastern states and still less so in the northwest prairie sections. The cultivated raspberries from the east are mainly of native origin, but show the influence of the west European type. However, these raspberries are not hardy for the prairie Northwest. Many years ago I began the work of growing thousands of seedlings of the red raspberry of South Dakota, North Dakota, Minnesota, Manitoba, and Saskatchewan. The work is still going on. By hybridizing with the standard cultivated varieties of raspberry a number of promising seedlings have appeared. The Sunbeam was the best in the first seven thousand seedlings, and the Ohta the best in the next six thousand. Both have become prominent over a large area. The object of this work is to develop red raspberries that will be hardy without winter protection. In 1923 six more varieties were offered with the same idea in mind. Therefore, they are not intended to compete with the larger fruited varieties that need to be protected by laying down the canes and covering with earth over winter. It may be that our future ideal hardy red raspberry will be derived exclusively from the pure native wild raspberry of the Northwest, but my experience with many thousands of seedlings indicates that this will be a slow process. Meanwhile, these hybrid varieties will be useful.

To obtain a hardy blackberry or dewberry it appears to be a much more difficult problem and the work is just in the beginning stage. The trouble is to find a hardy species to serve as a starting point.

Breeding Large Hardy Gooseberries

The largest gooseberries in the world are those grown in western Europe. A few years ago I succeeded in crossing these giant gooseberries with the wild

Sioux Valley gooseberry (*Ribes gracile*), from Lake Oakwood and Gary, South Dakota. This work was done in the Fruit-breeding Greenhouse at South Dakota State College. The European gooseberries did not live long even with special care, but long enough to make the cross. In the spring of 1924 the Sunset Gooseberry was offered for the first time as the result of this work. In 1925 ten more varieties of these hybrid seedlings were distributed. These eleven varieties indicate that large size of fruit, hardiness and productiveness of plant can be secured much more quickly by hybridization than by selection only. The pure native gooseberry has been carried through eight generations. I find that we can obtain large size of fruit, but they all have the fault of ripening through a long season while in the hybrids the fruit ripens more at the same time which is necessary from a commercial standpoint.

Developing the Wild Black Currant

The wild black currant (*Ribes floridum*) is abundant throughout the state. I have grown many thousand seedlings of this species as found at Lake Oakwood and Gary, South Dakota, through several plant generations, beginning in the fall of 1895. But in 1923 there was a decided break, and a number of plants appeared with fruit of remarkable size and so productive that they appeared worthy of propagation and introduction, although the berry that is ideal in quality has not yet arrived. The wild black currant is a good ornamental shrub with large yellowish white flowers in drooping racemes and smooth black fruit. One advantage of the wild black currant as a low shrub is that they endure more partial shade than many other shrubs. In European gardens this American species is considered worthy of a place in the ornamental shrub collection and it should receive equal consideration here at home. The foliage turns to a handsome brown red color in the fall.

The common black currant, *R. nigrum*, of northern Europe and Asia has not generally proven productive on the prairie uplands of the west. Perhaps better results can be obtained from these indigenous black currants, but the white pine blister rust may stop all future work with either species, at least in sections where the five-leaved pines are grown.

Conclusion

The foregoing will cover the main lines of my work in improving and importing fruits since 1895 at the South Dakota Experiment Station, and as Agricultural Explorer for the United States Department of Agriculture. I am working with many other plants such as alfalfa and roses but this will suffice to give the main idea: (1) That we should improve the native species whenever possible. (2) That we should import other species if improvement is to be expected from them.

STOCKS FOR HARDY FRUITS[1]

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A few years ago I read a description of a "new method" of grafting invented by a worker in one of our American experiment stations. The novelty—a kind of inarching—seemed familiar. Turning to a book on Roman Farm Management, I found that Varro, "most learned of Romans" had described the same process 2000 years ago, not as a new method but as one "recently suggested." Varro, author of six hundred and odd books, was a compiler, and cites in his treatise on agriculture fifty Greeks and Romans who had written before him, so that it is probable that his "recently suggested" process of grafting was practiced several hundred years before he wrote.

Should I attempt to tell you anything new about kinds of stocks, or any process of joining cions to them, some one of you would quickly catch me up and show that what I was palming off as original was "recently suggested" 2000 or more years ago. There are no new stocks; there are no new methods of joining stock and cion; there are few uses for any of the many stocks upon which hardy fruits are now grown to which they have not been put ages ago.

Yet much that is worth while has been learned in recent studies of stocks. The phenomena that our predecessors in pomology described were to them largely fortuitous. We have learned that most of the relations of stocks and cions are based on physiological laws, and to some extent we are able to predicate what will happen in combinations of specific stocks and cions. We have learned what the choice of stock should be for diverse soils, climates, and cultural practices. The experiences and practices of centuries, together with the new knowledge, is set forth admirably in bulletins, in the horticultural press, and in pomological texts of all countries where hardy fruits are grown. Yet, I think it may be said, for America at least, that there is no phase of pomology now so disturbing and troublesome as that of choosing and getting fruit-plants on proper stocks, a phase of our industry in which relations between the pomologist and the plant propagator are usually strained and often unpleasant. Further complications will soon be added because, whereas we have long imported most of our stocks, we must, because of a governmental prohibition on importations, begin at once to grow our own supply.

What is wrong with our stocks? How can the situation be bettered? These questions are to be the theme of my paper. But before they can be discussed, we must agree as to the use and functions of stocks.

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 17, 1928.

At this season of the year in every part of the northern hemisphere where hardy fruits are grown, armies of expert workman are found in plantations of young fruit trees budding so dexterously, precisely, and rapidly that their work is little short of marvelous. Every one knows that only by such consorting of stock and cion, by one of the many processes of budding and grafting, can fruit trees true to name be rapidly propagated.

Plants are delicate mechanisms, easily thrown out of gear, and in these adjustments of cion and stock now going on, and in the reactions of the one upon the other that follow, the resulting fruit plant must often be profoundly influenced; therefore these adjustments of top to root become very important to the product of the plant. It is a vital consideration that fruit growers and nurserymen know what these reciprocal influences of stock and cion are. Perhaps no other phenomena in pomology have been recorded so frequently and precisely. They have been examined, correlated, and set down many times by the best minds in pomology, so that I think we can agree on what the interrelations of stock and cion are:

1st. The stock may change the stature of the plant.

2nd. The form or habit of growth which many two-part fruit plants assume is influenced by the stocks.

3rd. The relations of species and varieties of the several fruits to soils may be changed by the stock.

4th. The stock may assist the cion to endure incompatible climates.

5th. Disease may be reciprocally transmitted between stock and cion.

6th. Yield may be modified by the stock in either increasing or decreasing fruitfulness.

7th. The time of bearing may be changed by the stock.

8th. Leafing and blooming may be hastened or retarded, and crop maturity and leaf-drop may be similarly affected.

9th. The color of the fruit may be changed.

10th. The size of the fruit is often increased by the stock.

11th. The stock may affect the quality of the crop.

12th. The stock may shorten or lengthen the life of the plant.

13th. The cion, in its turn, affects the size, depth, branching, and fibrousness of the stock.

The influences of the stock on the cion just set forth are for the most part quantitative and are due, we no doubt will agree, to modifications of vigor. Various stocks supply water and nutrients to the top in varying degree,—nearly all of the effects follow. Exceptions, possibly, are adaptability to soils, the modification of the shape of the top by the stock, and the modification of the root system by the cion. All of the other effects named may be brought about by modifications of cultural conditions which affect vigor. These influences of the stock and cion however, are vitally important to fruit-growers and must ever be kept in mind in choosing plants. The choice of stocks to secure these effects is nearly always a local problem. Special soils, climates, or purposes may require stocks of great vigor; another set of conditions, stocks of less vigor.

Yet, the matter of adjustment of stock and cion is not quite so simple as one might conclude. There is the further matter of congeniality or compatibility to consider.

Only species that are closely related can be consorted by budding and grafting. But in the case of many orchard fruits when the kinship is close, as, say, within a species, the plants resist all of the appliances of art to make a successful union, while, on the other hand, some species quite distinct seem fore-ordained by heaven to be joined. Perfect compatibility is secured only when a plant grafted on another behaves as if the stock were grafted with a cion of itself. Affinities between stock and graft can be determined only by actual test.

In these few brief paragraphs I have covered ground to which a volume, and a large one, might be devoted, with thousands of illuminating examples, many exceptions, and almost innumerable citations of authorities for the pros and cons. Indeed, my presentation of the subject of stocks, without the usual examples, exceptions, and citations may seem to you childishly simple. But I am not offering a technical discussion of stocks, appropriate as such a discussion might be in a congress of plant sciences, but, rather, I want to show, as can be done in fewer words than I have already used, a practical side of my subject which is of world-wide importance and therefore should also be of interest in an international congress.

The troublesome phases in the use of stocks to which I want to call your attention are those of present practices in the propagation of stocks.

As matters now stand in all of the countries where hardy fruits are grown, the production of young fruit plants is in the hands of one set of men, nurserymen; while their cultivation as fruiting plants in the orchard is in the hands of professional fruit-growers. Now unfortunately the immediate interests of the two trades are not always identical in the matter of stocks.

Thus, in the use of stocks in America, all but a wholly insignificant part of our trees are grown on seedling roots, the exception being dwarf apples, some pears on quince, and a few plums on Marianna. These seedlings are much more suitable to the nurseryman's business than to the fruit-grower's. The defects of variable stocks grown from seeds of unknown parentage are apparent to everyone in theory, and everywhere in practice; we shall never be sure of good stocks until all are grown vegetively or are raised from seed that will come true to type. Hatton and Grubb of East Malling, in work as admirable and conclusive as any that has been done in pomology in this century, have shown that stocks for all of our fruits can be grown vegetatively and advantageously to the fruit-grower. A few days spent recently at East Malling sufficed to convince me that in the future refinement of fruit growing we shall grow much of our stock from vegetative parts. The change from seed to layers, suckers or cuttings, as the case may be, will be long and slow. Meanwhile we must rely upon seedlings at least in part.

The seed now used for stocks for all hardy tree-fruits are unsatisfactory to fruit-growers, or would be if the fruit-grower knew what he was buying in the seedlings that come from them. Nor is the seed satisfactory to the nurserymen. It is always expensive, sometimes unobtainable, often untrue to name, and is

usually uncertain in viability. Their histories, for the most part, show plainly that it is a throw of the dice as to whether nurserymen get good or a poor seedling; the fruit grower a good or a poor tree.

American pomologists and nurserymen visiting Europe have generally reported poor seed in the stock-growing centers of France, whence most of our seedling stocks come, a condition which I had opportunity to verify the past spring. The seed supply, it was found, is exceedingly variable, depending upon crops of the fruits from which they come, labor, and prices received. The present supplies of the seeds most commonly used are from the following sources:

Apple and pear seeds come from cider pomace made in Normandy, the fruits for which grew on seedling trees of *Pyrus malus* and *P. communis*, although much of the pear seed may come from *Pyrus nivalis*, nearly worthless as a stock. Most of the Mahaleb seed comes from hedges in the fields of Lyons, France. Mazzard seed formerly came from mixed trees in Normandy, but the supply there became inadequate, and much Mazzard seed now comes from fruit preserving processes and is a mixture of sweet and sour cherry seed; these mixtures contain many non-viable seeds and of the seedlings produced many make poor or worthless stocks. Myrobalan plum seeds come mainly from northeastern Italy, where the fruit is used in wine-making.

Trees from these seeds show innumerable variations in type and vigor, and even granting that the cions worked on them tend to reduce variability, as I think they do, yet I believe and feel sure that most of you agree that much of the variability in orchards is due to variability in stocks.

A paternalistic government has announced through its Department of Agriculture the probable exclusion of foreign fruit stocks in 1930. After that time we shall have to import vast quantities of seeds of tree fruits. Here we run into further difficulties. Once seeds of tree fruits, especially of stone fruits, become thoroughly dry, they quickly lose vitality. Our experience at Geneva is, and I was told the French grower of seedlings had long ago learned, that the sooner the seeds are stratified, or placed in suitable storage after the harvest, the greater the number of germinations. Imported seed is, and without extraordinary care must continue to be, unsatisfactory.

If it be concluded that, for some years to come, it will not be feasible to grow stocks from vegetative parts, and all nurserymen with whom I have talked take that view, must we not make sure of a supply of seeds less variable and with a higher percentage of germination than those now imported from Europe? How may better seed be obtained for the millions of seedling stocks we must grow in America after 1930?

In growing various seedlings on our Experiment Station grounds, we find that seeds from certain varieties germinate freely and produce a uniform stand of vigorous seedlings, whereas seeds of other varieties of the same fruits give us none, a few, or a much smaller stand of poorer seedlings. Our best seedling apples came from McIntosh, Northern Spy, Ben Davis, and Rome Beauty. Seedlings from Bartlett are probably as good as any and far better than those from most other varieties of pears. Remarkably vigorous and healthy Mazzard stocks may

be grown from Downer's Late and Winkler sweet cherries. Morellos come fairly true to type and make vigorous trees, so that a good stock might be grown from some Morello for sour cherries. Mahaleb, on our grounds at least, is worthless for either sweet or sour cherries. Young's Golden and De Caradeuc furnish splendid types of Myrobalan plums. As long as a good supply of peach pits from mixed seedlings in Southern mountain regions can be had, growers of peach stocks should be content, but in case of need, seedlings of Crosby, Chili, and Salwey should make far better trees than miscellaneous seeds from canneries.

In my opinion the time is at hand when a lucrative business could be established in America in producing seeds solely for the nursery trade. There are now, I feel sure, varieties of all hardy fruits from which uniformly good stocks could be grown, and if not, selections from wild plants should be made and to these should be given varietal names, to be grown only for the purpose of furnishing seeds for stocks.

We all agree, I am sure, that the matter of stocks is of paramount importance in the growing of two-part fruit plants. Now that America must soon grow all stocks used in the country, thereby revolutionizing the nursery trade, since, as I have said, for many years nearly all stocks have come from Europe, it is important to start right. The professional pomologist of stations and colleges should lend every effort to help in this work. There is need, I feel sure all foreign fruit growers will agree, of revised methods of growing stocks in foreign countries. Shall we grow stocks from vegetative parts? If so, what and how? Or, shall we do better to continue with seedlings? If so, where shall we get the seeds? How shall we grow the seedlings? Am I right in my belief that experience and experiments have demonstrated pretty well what the relative merits of different stocks are for hardy fruits; that we know pretty well what the best methods of joining stock and cion are; but that we fall far short of our knowledge in practices.

EFFECT OF SIZE OF SEED ON PLANT PRODUCTION[1]

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The practical and theoretical importance of the quality of the seed sown upon the resulting crop was studied 50 years ago (1875–1885) and this revealed a need for critical examination, which last has been given in recent researches (1912–1925).

Some of the authors of the latter period of research (Delassus, Cummings) hold the view that there may be a *distinct* influence of size of seed on the yield, although the general trend of the work done by most investigators shows that there is a slight effect only, when heavier seed are utilized for planting.

The problem in question has been attacked also in my researches, and therefore I will present a brief account of them, in order to make my personal contribution to this problem.

The subject matter of these researches were peas, broad beans, and cabbage. The experiments with leguminous plants were performed during 1921, with cabbage in 1925, all under field conditions.

1. Pea (Pisum sativum)

The variety used was a French early variety called "Pois Michaux amelioré," German synonym, "Allerfrüheste Maierbse," which was quite uniform to type and bred true in 1919.

Three kinds of seed material were prepared after a careful weighing of each seed: large seeds of pea, of which the hundred-seed weight was 33.7 gm.; small seeds of pea, weighing 17.2 gm. per 100 seeds, and again seeds of pea with a total weight per 100 seeds of 16.5 gm. These last were obtained artificially from large seeds, which were deprived of cotyledons, the seed leaves being cut away in part from the dry seeds before germination.

The peas were sown April 12, on little plots (20 m.²), each of them accommodating 68 seeds. Germination occurred April 28, blossoming, May 18 to June 22, the ripe pods were harvested July 19. Each kind of seed was replicated three times. All the plants grew on sandy but fertile soil.

Ravages during pod ripening affected very much the reliability of results concerning yield, hence such data are of doubtful value. But the accuracy of the experiment was not disturbed if comparison of seed quality is considered. It is evident that there was no difference between the three groups in yield. For the large seeds the result was 26.6 ± 0.5 gm. for 100 seeds, for small whole seeds

26 ± 0.4 gm. and for those with half-cotyledons 27.8 ± 0.2. The selection used did not exert any influence. It is obvious that the seed quality of the peas in question was already firmly fixed. Since, as far as we know this commercial variety, it showed the following hundred-seed weights: 1919—26.4 ± 0.8 gm., 1920—25.8 ± 0.3 gm., 1921—26.9 ± 0.7 gm. The pods could be grouped into three classes as respects length: long (8–6 cm.), medium (6–4 cm.), and short (4–2 cm.). A total of 8800 pods was examined. The percentage of each class in the whole yield of pods was as follows:

	Long	Medium	Short
Large seed.	43.4	49	7.6
Small whole seed	40.4	52	7.6
Seed with half-cotyledons	35.7	58.6	5.7

This review suggests that the influence of size of seed was slight when it affected pod productiveness. The ratio among the classes of pods changed but little in the last group of seed material.

2. Broad Beans (Vicia Faba major)

The variety used was a commercial, small-podded variety "Mazagan," cultivated under field conditions till 1919. A strain quite uniform and bred during 1919 and 1920 was used in 1921.

Four kinds of seeds, in respect to weight, were selected: Large whole broad beans, hundred-seed weight 115 gm.; small whole broad beans, hundred-seed weight 33 gm. The differences between the seed groups were so distinct that one would expect some influence on the seed yield. With the last two groups the cotyledons were cut away in the dry seeds, before the sowing time, as in the case of peas.

The seeds were planted in plots (20 m.²) each containing 68 plants. The broad bean appeared above ground May 2, and blossomed May 30 to July 20; the gathering of pods took place August 9; the period of vegetation was shortened in consequence of rainless weather.

The effect of size of seed was not deniable in the early growth of the plants; in this period, ending with blossoming, the height of plants was in direct accord with the size of the seed. The differences decreased approaching maturity and

TABLE 1. EFFECT OF SIZE OF SEED ON YIELD OF BROAD BEANS

	Height of plant, cm.		Total number of pods per plant		Weight of 100 seeds, gm.		Yield of seed per plant, gm.	Number of plants
	$A \pm e$	Mo	$A \pm e$	Mo	$A \pm e$	Mo		
Large seed (whole)	108 ± 0.6	103.5	29 ± 0.5	28	92.5 ± 0.7	85	53.7 ± 3.8	188
Small seed (whole)	95 ± 0.5	103.5	31.4 ± 0.5	33	71.6 ± 0.5	65	53.2 ± 2.3	189
Large seed (halved)	101 ± 0.7	103.5	27.3 ± 0.5	28	82.7 ± 0.7	85	51.7 ± 1.1	183
Small seed (halved	91 ± 0.6	103.5	26 ± 0.5	28	69 ± 0.5	65	41.8 ± 1.5	165

at harvest time disappeared completely. The data are given in Table 1 (arithmetic means and modes).

The behavior of the broad bean is *like* that of the pea. The selection of seed has given no differences in yield in three kinds of seed planted, a moderate diminution took place when the smallest seed was used, but it may be said that the ratio between the largest and the smallest in seed sown was 100:28, while the progeny differed in yield as 100:78.

The height of all plants was alike. The number of pods showed no influence of seed planted. The seed quality was alike in groups that originated from small whole and small halved seed as well as in those from large whole and large halved seed. It clearly shows no influence of the removal of cotyledons.

The differences among the seed groups did not *disappear*, their significance concerning hundred-seed weights of the yield being maintained. It may be remembered the average hundred-seed weight of the variety "Mazagan" was 77.2 gm. in 1919, 75.4 gm. in 1920, and 76.8 gm. in 1921. But it shows at a glance that the limits of variation of this character are narrower in the seeds harvested than in the seeds sown. We shall show this fact in Table 2.

TABLE 2. DISTRIBUTION OF 100 SEEDS WEIGHTS IN GRAMS

	25 34	35 44	45 54	55 64	65 74	75 84	85 94	95 104	105 114	115 124
Seeds sown: small, halved	32.5									
Seed sown: large, halved				57.5						
Seed sown: small					65.					
Seed sown: large										115.
Seed yielded: small, halved					69.					
Seed yielded: large, halved						82.7				
Seed yielded: small					71.6					
Seed yielded: large							92.5			

There seems to be an advantage in using smaller seeds, because the ratio between the quantity of seed sown and yielded was, in large and small seed, 1:44 and 1:79, respectively.

3. Cabbage (Brassica oleracea capitata)

Peas and broad beans are annual plants because the period of production at the end of a single season is the end of their vegetation too. The results cited in the literature were all obtained with annuals, and it seemed desirable to use a biennial. For this purpose the attempt is made to learn something of the product of cabbage, a biennial and typically cross-fertilized species, under conditions of field trials, which might help to clarify the question of the effect of size of seed on plant production in the first year of growth.

The seed of a population of Brunswick short-stem cabbage was chosen. This strain has proved uniform and true to type when cultivated during 1923. The cabbage seeds were graded on screens and there were distinguished two kinds of

size. Large seeds, with diameters 2.5 to 3 mm. (average, d = 2.75mm.) and small seeds, limited to 1.5–2 mm. (average d = 1.75 mm.). Their volumes, when calculated as spheres $(= (d^3/6)\pi)$ were for 100 seeds 10850 mm³. for large seed, and 2720 mm³. for small seeds. The hundred-seed weight was (in average of six lots of each kind) 0.808 gm. and 0.363 gm. Hence, the volume ratio was 4:1 and weight ratio 2:1, approximately. It seemed that differences between sizes of seeds were quite sufficient to enable one to expect interesting results.

To attack the problem, four standard treatments in cabbage culture were compared. (1) Large seed, the seed bed and the field plots fertilized; (2) small seed, the bed and the plots fertilized; (3) large seed, the bed and the plots unfertilized; (4) small seed, the bed and the plots unfertilized.

The seed was sown in the open seed bed in the garden. The bed was divided into four parts, each of them covering one square meter; two parts received, before sowing, a fertilizer supply as follows: 45 gm. of sulphate of ammonia, 80 gm. phosphate (15 per cent P_2O_5) and 60 gm. potassic salts (40 per cent K_2O). The cabbage seed of the first and of the second treatments were sown on them. The two remaining parts of the seed bed received no fertilizers and therefore received the third and fourth treatments.

The experiment was started March 28, 1925, sowing on each part of the bed 25 grams of cabbage seed broadcast. The germination began, and the seedlings appeared above ground April 7, at once on all parts of the bed, although the germination was earlier when large seeds were planted; nevertheless, after four weeks' growth, the parts of the bed were very uniformly covered with seedlings, which differed in size very much on each of the beds. To determine differences due to the size of seed and to the fertilizers, measurements and weighings of cabbage seedlings were made May 27, before planting them into the field plots.

The cabbage was transplanted May 28, and it must be noticed that seedlings from outside rows were invariably discarded, the aim being to obtain the most uniform stock of plants possible. Each treatment was planted on four parallel plots, alike in shape, each being 50 square meters in size. The seedlings derived from the fertilized bed were transplanted to eight fertilized plots. A moderate food supply was given these plots, consisting of 1.6 kg. sulphate of ammonia, 2.8 kg. phosphate, and 2.8 kg. potassic salts per 100 square meters. The seedlings originating from the unfertilized bed were not furnished with nutrient salts. It may be mentioned that the field prepared for cabbage culture in 1925 was manured with stable manure (± 50.000 kg. per ha.) in the fall 1923; moreover, the previous crop, early potatoes in 1924, did not exhaust the soil or decrease the soil fertility. The experiment was carried out on 16 plots of sandy soil with good water conditions and sufficient organic matter. The plots were arranged in 2 zones of 8 plots; on each plot there were 150 plants set 50 by 55 cm. Shallow cultivation was given during the season and weeds were kept down by hand hoeing after cultivation ceased. No evidence of fungous infection and of injurious insects was found on examination during the summer.

The problem of the effect of size of seed in cabbage is considered in three sections: (A) Analytical study of seedlings; (B) the value of plot yields, and (C) description of the cabbage plants (yielded from each treatment).

A. ANALYTICAL STUDY OF SEEDLINGS

After the soil was washed from the roots, the young plants were dried with blotting paper, weighed, and the length and the breadth of blade of the largest leaf were determined. The differences in regard to these characters are recorded in Table 3.

TABLE 3. FREQUENCY DISTRIBUTIONS OF SEEDLING WEIGHTS; 60-DAY STAGE (27. V.); %% OF THE NUMBER OF PLANTS

Origin and treatment of seedlings	-2λ	-1λ	V	$+1\lambda$	$+2\lambda$	$+3\lambda$	$+4\lambda$	$+5\lambda$	$+6\lambda$	$+7\lambda$	Average weight of seedling gr.	Number of plants weighed
Large seeds: the bed non-manured	—	— —	44.3	26.7	13.7	9.2	4.6	1.5	—	—	2.6	129
Small seeds: the bed non-manured	—	—	44.5	28.2	20.3	4.7	1.6	0.7	—	—	1.1	128
Large seeds: the bed manured	1.5	15.5	24.8	22.5	20.2	5.4	4.6	1.6	1.6	4.3	4.6	129
Small seeds: the bed manured	4.7	16.4	38.3	19.5	11.7	7.0	1.6	0.8	—	—	2.0	128

The amount of the food stored in the seed is of major importance for early growth; however, the beneficial effect of fertilizing is doubtful. A consideration of Table 3 indicates that there are unquestionably significant differences in favor of large seed. The ratio of the seedling weight obtained from large seed as compared with that resulting from small seed is 230:100, that is, quite the same as the ratio of hundred-seed weight, namely, 220:100. The relation between weight of seedlings developed on fertilized and unfertilized beds is narrower than that mentioned above; it is 178:100. This fact indicates that the developmental process of cabbage is dependent in high degree during its first period (for instance, 60 days) on food quantity offered by the seed, and this relation is of higher value than that of increase of nutrient salts in the soil.

The frequency distributions of seedling weight involve some interesting questions. They are presented in Table 3 as a means of facilitating the comparison of the four treatments. The number of individuals in every class is submitted in percentage of all individuals weighed in each lot; the deviations from the mode (V) are calculated in class units (λ), which were chosen for large seed seedlings $\lambda = 1$ gram, and for small seed seedlings $\lambda = 0.5$ gram.

Different factors may influence the rate and the form of development, hence the size and weight of the young plants, if they are grown from several lots of graded seed sown broadcast in the bed. The result will always be that the variation in such a group is *continuous* and that the variation of the resulting plants in respect to such a character as weight, when expressed graphically, will yield a typically normal Quetelet's curve. And really that is what happened regarding the curves of seedling weight when the seedlings developed in fertilized beds without regard to the seed size.

Some peculiarities come up as we consider the variation of the weight of seedlings kept on unfertilized beds. The curves here observed are not in any case Quetelet's or binomial curves, that is, they are not symmetrical, but are markedly skew curves (Figs. 1, 2), in which the mode lies at the lower range end, and the deviations from the mode are exclusively positive. What is the cause of this extraordinary behavior of variability, distinguishing in a broad way the
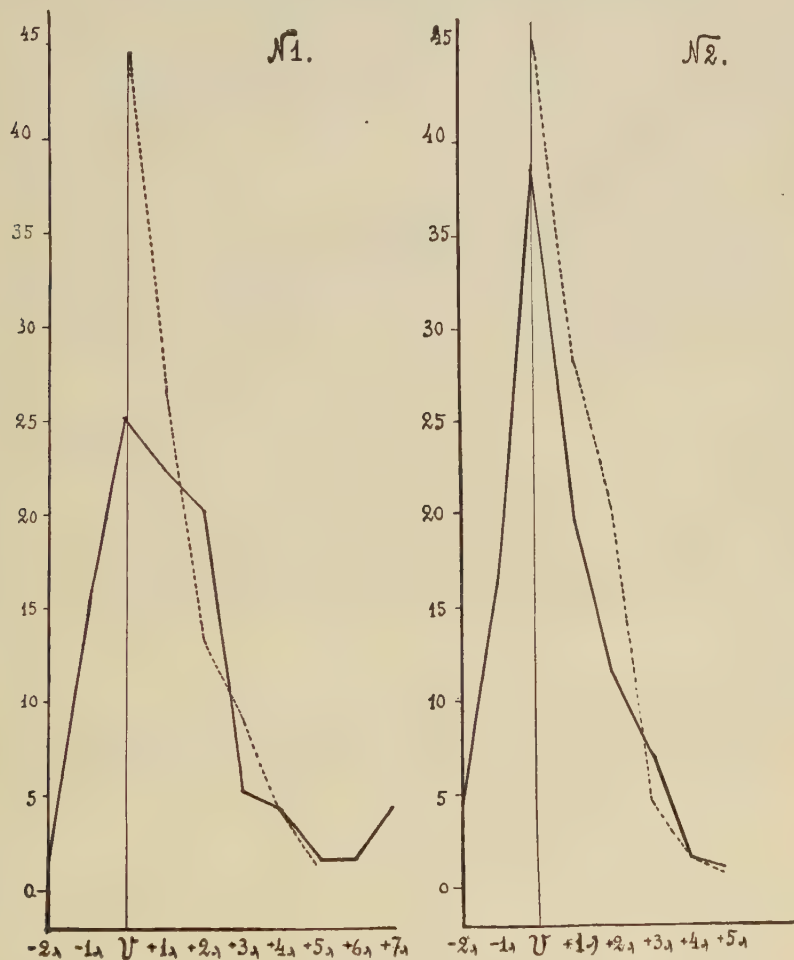

Fig. 1, 2. (1) Large seed: broken line, bed non-manured; continuous line, manured. (2) Small seed: broken line, bed non-manured; continuous line, manured. (See Table 3.)

two means of development? As far as I can suggest, the following explanation may help to understand this fact. The addition of nutrient salts to the soil of the bed changes the opportunities for the development of the young plants. They profit during early growth from the food accumulated in the seed leaves and from the dilute salt solutions too. It is obvious that these are favorable conditions for increase of size, hence we find the greater average weight of seed-

lings, and some of them became extremely large, $(+6\lambda, +7\lambda)$. In the other case, the soil fertility is poorer, and with the lack of nutrient salts the young plants must cover their food requirements from the seed supply alone. It is quite probable that these seed supplies are equal, so that all seedlings, or most of them, approach the same weight, what corresponds to initial seed weight, and the seedlings become larger from heavy seed and smaller from light ones. In these lots the mode gives the lower limit of variation, and deviations that are noticed may find their origin in favorable opportunities for seedlings in the later period of growth, when the food-stuffs of the seed are exhausted completely.

It is evident that a more detailed analysis of the data is wanted, but that does not relate closely to the aim and scope of this report and is the subject matter of an investigation in progress.

A short study of the further development of the plants during summer must precede an adequate evaluation of the yield in autumn; it is necessary to know this development in order to understand later facts. The most important accomplishment so far was the determination that the differences observed in seedlings became gradually invisible between plants derived from large and small seeds.

B. THE VALUE OF CABBAGE YIELD

The experimental cabbage was harvested Oct. 5, that is 190 days after sowing in the seed bed and 130 days after setting into the field. The green weight of the plants of each plot was determined and these records are called rough yield. Data relating to the quantity of marketable heads reported herewith have great economic significance. They are obtained by trimming the heading plants, and rejecting leaves that failed to form heads, as well as stalks.

The arithmetic (A) means of yields are given in Table 4, accompanied by standard errors (e).

TABLE 4.

The harvest time, Oct. 5, 1925	Total yield of green weight per plot (area 50 sq. m.)	Yield of marketable heads per plot (area 50 sq. m.)	Percentage marketable heads in total yield (average)	Percentage of plants non-heading (average)	Percentage of plants lost on one plot (average)	Number of heading plants on one plot (average)
Origin and treatment of plants	$A \pm e$ kg.	$A \pm e$ kg.				
Large seeds: the bed and the plots non-manured	175 ± 6.9	82.5 ± 3.3	50 ± 1.7	15.0 ± 2.0	2.5 ± 0.5	123
Small seeds: the bed and the plots non-manured	177 ± 4.7	100 ± 3.9	50 ± 0.6	10.7 ± 1.2	1.8 ± 0.3	131
Large seeds: the bed and the plots manured (N+K+P)	235 ± 8.4	124.5 ± 6.5	53.5 ± 1.3	9.1 ± 1.5	1.8 ± 0.5	131
Small seeds: the bed and the plots manured (N+K+P)	231 ± 6.0	136 ± 2.5	60 ± 1.3	7.8 ± 0.7	3.6 ± 1.8	133

There are very striking results grouped in Table 4, because they show at a glance that there is no marked difference in cabbage production in the first

year of vegetation due to the grade of seeds, whether heavy or light. The differences in the green weight yields are smaller than the errors.

A real advantage is manifest, when supplying the field with fertilizers, but it was not our main idea to investigate the fertilization response and this, therefore, might be neglected in this report. The yield of marketable heads is alike throughout plots on the fertilized field. We find a distinct difference in favor of plants originating from small seeds ($+17.5 \pm 4.5$ kg.), if we consider the yield of marketable heads of non-fertilized plots. If it is asked what contributes to such an effect, we can reply that it was related to the high percentage of marketable heads in regard to the whole plant-weight. The strain of Brunswick short-stem cabbage cultivated without fertilizers gave 41 per cent of the whole yield in rejected leaves and stalks, when the plants were derived from light seeds, against 50 per cent of refuse parts, when the plants originated from heavy seeds. The same occurred on fertilized soil. It may be cited, for comparison, that some strains of Brunswick cabbage yielded in our field trials in 1921, 1922, and 1923, 47–52 per cent of the whole amount as refuse material. The seed sown in those trials was after the elimination of light seed, and this selective treatment caused a distinct decrease of marketable heads. In consequence, there will be no practical gain in cabbage yield under truck farming conditions from the application of large size seed selection of cabbage.

The further question arises, does the size of the seed affect the heading process in the cabbage? The answer will be found in Table 4, in noting the percentage of plants that failed to form heads. Of course there were but few plants which produced only leaves instead of heads, and it was not dependent on size of seed, rather there should be noticed advantages in heading process obtained by fertilizing, as it is evident from differences in favor of fertilized plots ($+6.8 \pm 2.5\%$ and $+2.9 \pm 1.4\%$).

Great uniformity of life vigor and immunity against fungous diseases and injurious insects was observed in the cabbage plants on every plot, as shown in Table 4. The losses are small and did not vary according to size of seedlings nor soil fertility.

C. DESCRIPTION OF THE CABBAGE PLANTS

This description was based on 196 individuals with each treatment, accounted in four lots of 50 specimens of each plot. The characters taken into consideration were:

1. Weight of leaves, which failed to form heads, rejected by trimming.
2. Weight of trimmed marketable head.
3. Horizontal diameter of the head (d_1).
4. Vertical diameter of the head (d_2).
5. Volume of the head $= (d_1^2 \cdot d_2/6) \cdot \pi$.
6. Weight of whole plant (excepting roots).
7. Per cent of marketable heads in whole plant weight.
8. Coefficient of the head shape (ratio: (horizontal/vertical) diameters).
9. Coefficient of the head firmness (ratio: (volume/weight) of head).

In order to obtain the desired data incomparable form and to present them easily the biometrical method was used (Pearl '14). The subject matter is arranged in two divisions. In the first (a) division the means, standard deviations, and coefficients of variability are studied; in the second (b) division degree of interrelation between characters of cabbage as shown by correlation of coefficients and correlation ratios.

(A) THE MEANS AND VARIABILITY OF CHARACTERS

Reference to Table 5 shows the conformity and differences among plants resulting from every treatment. An estimation of differences three times greater than their errors is only made when based on conclusions reported herewith. The plants developed from large seed, as compared with those from small seed, displayed an increase in the weight of leaves rejected by trimming, a decrease of the percentage of heading leaves in the whole plant weight, and possessed lessened firmness. However, the weight of cabbage head, the weight of the whole plant (excepting roots), the diameters, and the shape of head were alike for plants of both kinds of seed size. The set of cabbage acquired from small seeds was superior to that of large seeds, because, the weight of head being equal, it possessed better qualities as a marketable product, which is important in olericulture.

(B) CORRELATED CHARACTERS IN CABBAGE

The assembled data also offered the opportunity to study the interrelations of plant characters for which there are presented in Table 5 the coefficients of correlation (r) and the correlation ratios (η). The quantitative examination of correlations in cabbage was made first, probably, by the author of the present report, in his description of some commercial varieties of cabbage, where there were studied 29 interrelations and 17 correlation coefficients. At that time there were distinguished two kinds of correlations: physiological correlations, almost always very high, but not significant in breeding work; also essential breeding correlations, the presence of which facilitates the breeding treatment.

In the present account of correlations made, it is only to the latter kind that attention is called, and ten important pairs of characters are submitted. For each pair three computations were prepared: r, $\eta(x/y)$, and $\eta(y/x)$. In many cases the r were lower than the η. It occurs to one that some of the low values for r may be due to non-linear regression. To be convinced of that, the straightness of the regression line was proved by means of Blakeman's test (Pearl '14). There were, however, not many indications that a curve of a higher order would describe the results better than a straight line and we may conclude in most cases that the regression was certainly linear, excepting five interrelations as follows:

1. Weight of rejected leaves and weight of marketable heads (for small seeds, fertilized plots).

2. Weight of rejected leaves and coefficient of head firmness (for small seeds, unfertilized plots).

3. Horizontal diameter of head and coefficient of head shape (for small seeds, fertilized plots).

TABLE 5.

The harvest time: Oct. 1, 1925. The arithmetic mean ± standard error (A ± e); n = 196 plants

Origin and treatment of plants	Weight of leaves which failed to form heads; rejected by trimming	Weight of trimmed marketable head	Weight of the whole plant (without roots)	Percentage of marketable head in whole plant weight	Horizontal diameter of head	Vertical diameter of head	Coefficient of the head shape	Coefficient of the head firmness
	gr.	gr.	gr.	%	cm	cm.		
Large seeds; the bed and the plots non-manured	498 ± 11.3	925 ± 26.3	1410 ± 34.3	64.8 ± 0.05	16.5 ± 0.2	8.6 ± 0.1	1.93 ± 0.013	0.74 ± 0.005
Small seeds; the bed and the plots non-manured	388 ± 9.4	990 ± 29.3	1372 ± 39.2	72.7 ± 0.06	16.2 ± 0.2	8.7 ± 0.1	1.88 ± 0.016	0.79 ± 0.005
Large seeds; the bed and the plots manured (N+P+K)	551 ± 13.8	1263 ± 38.6	1800 ± 48.5	69.3 ± 0.07	18.1 ± 0.2	9.3 ± 0.1	1.97 ± 0.016	0.76 ± 0.006
Small seeds; the bed and the plots manured (N+P+K)	452 ± 11.7	1341 ± 36.8	1780 ± 42.5	75.6 ± 0.05	18.2 ± 0.2	9.6 ± 0.1	1.92 ± 0.017	0.79 ± 0.005

4. Horizontal diameter of head and coefficient of head firmness (for small seeds, fertilized plots).

5. Horizontal diameter of head and coefficient of head firmness (for large seeds, unfertilized plots).

It is interesting that non-linear regression occurs when plants from small seeds are studied and when correlations are assigned to characters expressed in formulas (coefficients of shape and of firmness) instead of direct measurements.

There is the following arrangement of correlations, based on their average numerical value (the first the highest):

1. Horizontal diameter of head and percentage of marketable heads in whole plant weight.

2. Weight of leaves rejected by trimming and weight of marketable heads.

3. Horizontal diameter of head and coefficient of the head shape.

4. Weight of leaves rejected by trimming and coefficient of the head shape.

5. Weight of marketable heads and coefficient of the head shape.

6. Weight of marketable heads and coefficient of the head firmness.

7. Percentage of marketable heads in whole plant weight and coefficient of the head firmness.

8. Weight of leaves rejected by trimming and coefficient of the head firmness.

9. Coefficient of the head shape and coefficient of the head firmness.

10. Horizontal diameter of head and coefficient of the head firmness.

The correlations counted herewith are quite large, as they must be in order to make averages for every plant treatment. We have for correlation ratios for plants from large seeds and fertilized plots: $\eta = +0.360$; for plants from small seeds and fertilized plots: $\eta = +0.392$; for plants from large seeds and non-fertilized plots: $\eta = +0.318$; for plants from small seeds and non-fertilized plots: $\eta = +0.383$.

To give a short and clear review, correlations have been included in Table 6, after determining their height as follows: α, very high (0.750–0.500); β, moderate almost $< 3e$ (0.199–0.001). The advantage of calculating correlation ratios (η) instead of correlation coefficients (r) is clearly shown. Many of the interrelations classified in the group δ, if counted as r, should be removed from the group γ, β, or even α, if counted as η. Therefore, many doubtful correlations could be appreciated as such, when the latter calculating method has been applied.

The effect of the four standard treatments of cabbage culture might be studied in connection with their influence on the degree of correlative junction. For this aim it is desirable to divide the correlations into two parts: one containing α and β coefficients and another containing γ and δ. This division is shown in the brief summary added below.

	Plants from large seeds, unfertilized plots	Plants from small seeds, unfertilized plots
Coefficients α and β:	13	14
Coefficients γ and δ:	17	16

TABLE 6.

X (Correlated characters in Brunswick short stem cabbage)	Y	r ± e	$\frac{\eta x}{y} \pm e$	$\frac{\eta y}{x} \pm e$	r: L.N.	r: S.N.	r: L.M.	r: S.M.	$\eta_{x/y}$: L.N.	$\eta_{x/y}$: S.N.	$\eta_{x/y}$: L.M.	$\eta_{x/y}$: S.M.	$\eta_{y/x}$: L.N.	$\eta_{y/x}$: S.N.	$\eta_{y/x}$: L.M.	$\eta_{y/x}$: S.M.
1. Weight of leaves which failed to form heads; rejected by trimming	Weight of the trimmed marketable head	+.497 ± .054	+.58 ± .047	+.58 ± .047	α	α	α	α	α	α	β	α	α	α	α	α
2. Weight of leaves which failed to form heads; rejected by trimming	Coefficient of the head shape	+.345 ± .063	+.39 ± .061	+.37 ± .062	β	γ	β	β	β	β	β	β	β	γ	β	β
3. Weight of leaves which failed to form heads; rejected by trimming	Coefficient of the head firmness	(+.007 ± .071)	+.26 ± .066	+.22 ± .068	δ	γ	δ	δ	δ	δ	γ	δ	δ	γ	δ	γ
4. Weight of the trimmed marketable head	Coefficient of the head shape	+.228 ± .068	+.35 ± .062	+.30 ± .065	γ	δ	γ	γ	δ	β	β	β	γ	β	γ	β
5. Weight of the trimmed marketable head	Coefficient of the head firmness	(+.197 ± .069)	+.24 ± .067	+.29 ± .065	δ	δ	γ	γ	δ	γ	β	γ	γ	β	β	γ
6. Horizontal diameter of head	Per cent of marketable head in whole plant weight (without roots)	+.557 ± .049	+.63 ± .043	+.59 ± .046	α	α	α	α	α	α	α	α	α	α	α	α
7. Horizontal diameter of head	Coefficient of the head shape	+.420 ± .059	+.50 ± .054	+.46 ± .056	β	β	β	α	β	β	α	α	α	α	α	α
8. Horizontal diameter of head	Coefficient of the head firmness	(+.026 ± .071)	(+.11 ± .070)	+.05 ± .071	δ	δ	δ	δ	γ	δ	γ	δ	δ	δ	γ	δ
9. Percentage of marketable head in whole plant weight (without roots)	Coefficient of the head firmness	(+.127 ± .070)	+.25 ± .067	+.26 ± .066	δ	δ	γ	δ	γ	δ	γ	γ	δ	δ	γ	δ
10. Coefficient of the head shape	Coefficient of the head firmness	(+.153 ± .070)	+.23 ± .067	+.26 ± .066	δ	δ	δ	δ	γ	δ	γ	γ	γ	γ	γ	β

	Plants from large seeds, fertilized plots	Plants from small seeds, fertilized plots
Coefficients α and β:	16	16
Coefficients γ and δ:	14	14

This item argues that there was no influence of the size of seed on the degree of correlations calculated from resulting plants. It supports the conclusion that there was an effect of soil fertility on correlation height, because they were greater on richer soil (fertilized plots) than on a poorer one (unfertilized plots).

Conclusions

The investigations cover some horticultural plants of annual and biennial habits, as well as some self- and cross-pollinized forms.

The peas (Allerfrüheste Maierbse) (Pois Michaux amélioré) and broad beans (Mazagan) give the following responses to the problem in question:

1. The differences due to seed size may be distinguished during the early growth of the plant but is no longer evident when blossoming begins.

2. The productiveness of peas and broad beans, based on the number of pods per plant, and seed weight, does not diminish when using light or heavy seed material.

3. The investigation of cabbage (Brunswick short stem) had as an aim to study the behavior of a biennial and cross-pollinized species during the first vegetative year. Observations for a number of seasons and for a number of commercial varieties of cabbage should be made to settle definitely the question touched upon in this paper. However, the following conclusions seem justified:

(a) The size of seed influences the size of the seedling during a 60 day stage.

(b) The effect of size of seed disappears during the time of field growth of cabbage.

(c) The productiveness of cabbage is not dependent on the size of seed planted. From small seeds develop plants giving yields as high as those from large ones. The quality of the yield in question is better when small seeds are sown; in that case the head firmness is greater as well as the percentage of marketable heads.

(d) There will be no practical gain in cabbage culture under truck farming conditions from using large seed and rejecting the small seed.

(e) The size of the seed does not influence the degree of the correlations shown by the adult cabbage plant.

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INSTRUCTION IN LANDSCAPE GARDENING IN AMERICAN COLLEGES: A REVIEW AND CRITICISM[1]

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Approximately 50 colleges, universities, and technical schools in the United States are now giving a total of several hundreds of courses in landscapes gardening.[2] These courses have practically all grown up within the past 25 years, and their propagation visibly continues. A phenomenon so interesting as this deserves some examination. We who are connected with work in this field ought to elucidate for ourselves the underlying motives, and we ought further to consider whether these motives are sound and whether present teaching practice tends toward an adequate realization of our purposes.

EXTENT OF PRESENT TEACHING

In a survey made in 1921[3] it was found that 42 institutions were giving instruction of college grade in the field of landscape gardening. Of these 17 offered professional courses; in the remaining 25 institutions intsruction was non-professional or cultural.

The institutions giving professional instruction were:

> University of California
> Cornell University
> Cambridge (Mass.) School (for women)
> Harvard University
> University of Illinois
> Iowa State College
> Lowthorpe (Groton, Mass., for women)
> Maryland University

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 17, 1926.

[2] The term "landscape gardening" is used here as synonymous with "landscape architecture" or "landscape engineering." The term "landscape architecture" is approved by the weight of professional use in America; but "landscape gardening" is still the one employed in common speech and in a majority of the colleges.

[3] C. S. Hill, Ed., Second National Conference on Instruction in Landscape Architecture held at Harvard University. Report published at University of Illinois, 1921. The section of the report here quoted was prepared by a committee, Prof. H. V. Hubbard, Chairman. This report is adopted as the statistical basis of the present discussion. Figures have been checked but not changed. It is believed, however, that there have been 2 or 3 additions since 1921 to the number of institutions giving instruction in landscape gardening, in both the professional and the non-professional groups.

Massachusetts Agricultural College
Michigan Agricultural College
University of Michigan
Ohio State University
Pennsylvania State College
Syracuse University
Texas Agricultural and Mechanical College
Washington State College

Origin of Courses

An examination of the origin of these courses brings to light some surprising facts and suggests some curious reflections. A classification may be made with considerable accuracy indicating the schools in which this work in landscape gardening had its inception. The figures are as follows:

College of Agriculture	32
College of Science	4
College of Arts	1
College of Architecture	1
College of Engineering	1
College of Forestry	1
Independently	2
	—
	42

The entry for "colleges of science" here includes Vassar College, Wellesley College, and Smith College, all women's colleges where some instruction in landscape gardening is given in the department of botany. Those entered "independently" are Cambridge School and Lowthorpe, both private schools for women, where the work was established for its own sake and on its own basis. It may seem fair to omit these five anomalous cases from the present comparison.

If this exclusion be permitted it then appears that science, arts, architecture, engineering, and forestry have given the United States one school each in landscape gardening while the colleges of agriculture have produced 32. These figures are not merely fair; they give a distinctly moderate statement of the leadership of the agricultural colleges in this field.

Now landscape gardening is an art of many affiliations. It has in it elements of horticulture; it has close associations with architecture; its professional practice requires a considerable knowledge of engineering; finally it is a fine art and all its most fundamental principles, are shared by music, painting, and sculpture. As to its principles, therefore, it ought to grow out of the fine arts and should be expected to originate, as a college subject, in a school of fine arts. As to its practice it should derive from engineering (and yet more from engineering plus architecture) rather than from agriculture. Indeed, on all grounds of theory agriculture is about the last source from which such a germination should be prophesied.

Yet the facts utterly belie this expectation. In American colleges and universities landscape gardening is clearly the offspring of agriculture. Why?

I believe that the answer is, subject to many quite minor qualifications, simply that the agricultural colleges have had a greater interest in these matters and a stronger initiative. Much might now be said with respect to both this interest and this initiative; but such comments would partake strongly of the quality of personal opinion, and perhaps they were better reserved. The facts themselves are so striking that they can not be ignored.

Future Affiliations

So much for origins. What of the future?

It is my enthusiastic belief that landscape gardening can be and should be widely taught as a culture subject in colleges of every sort and even in high schools. In the administration of these brief non-professional courses the question of affiliations is of very slight importance. The only consideration which matters very much is the teacher. We must all pray for good teachers.

But in the schools where professional training in landscape architecture is attempted the problem of relationships may be fairly serious. Here the natural connections between landscape architecture, architecture, and the fine arts have seemed so powerful as to move many teachers to seek these (seemingly) more natural associations. We thus have the phenomenon in some institutions of a course migrating from its original nest to perch upon a distant bough. For illustration, a course in landscape gardening might originate in a department of horticulture in an agricultural college. After a few years it outgrows the home department and sets up by itself as an independent department of landscape gardening. After another period it may move quite out of the college of agriculture to seek a home in a school of architecture or of fine arts. All these steps have been illustrated in recent American history.

Where should professional landscape architecture, therefore, be taught? This question is not merely interesting; it is serious.

It can hardly be said as yet that the colleges of arts or architecture or fine arts have done anything on their part to justify in a practical way the leaning of landscape architecture in their direction. However obvious may be the relationships in theory it appears in practice that these colleges have little to offer in moral support, and still less in financial support, to professional instruction in landscape architecture.

Meanwhile, it would seem that the sympathy which led the agricultural colleges to conceive and the energy which enabled them to bring to birth so overwhelming a majority of the courses in landscape gardening, and the interest which still actuates them in maintaining a large majority of the most effective schools in this field, may fairly be trusted for the future. In short, while landscape architecture may have no very strong natural affiliations with horticulture, yet the schools of agriculture have proved to be such competent foster mothers (and we can only ungraciously deny them the closer relationship of direct motherhood) that we may fairly expect to maintain this relationship into a long future.

Ideals of Landscape Gardening

Such a strong and germinative movement as that briefly sketched above must have within it some impelling idealism. What then is American landscape gardening hoping to do for American life?

A recent attempt to answer this question[4] from the standpoint of the professional landscape architect has set forth 3 proximate objectives:

1. To make snug, comfortable, and beautiful homes.
2. To make clean, healthful, and beautiful cities.
3. To protect and interpret the native landscape.

These ideals obviously have high social value, and if they are being in any reasonable degree realized by American landscape gardening then this art may well occupy a prominent place in college curricula. As a matter of fact these objectives are clearly recognized and loyally followed by practically all members of the profession with very creditable results.

There is some doubt in the mind of the present writer whether these same ideals are as clearly pictured in the minds of college teachers and administrators — the men who have brought to birth the college courses already enumerated. In general, it seems that the prevailing idea with these men has been to realize the beauty of plants as applied to home decoration, making landscape gardening a minor branch of horticulture. While this is all very good, it is not adequate. It is far less comprehensive, and less clearly socialized, than the professional ideals stated above.

Landscape gardening should be a cultural subject to 100 college students for every one who studies it professionally, just as art now is. As a cultural subject it should emphasize the social value of the objectives already mentioned. It should earnestly seek also two other objectives:

1. To make order and beauty in the home a means of personal enjoyment and personal culture.
2. To realize the universal and incomparable beauty of the native landscape, making this great beauty a part of every day life and of personal enrichment.

The experience of several good teachers has shown that these ideals of social value and of personal culture can be measurably approached by wise instruction in non-professional courses in landscape gardening.[5] It seems important that all non-professional courses should be focused definitely upon such cultural ideals rather than to be diverted to any sort of professional or "practical" instruction.

Principles Governing College Instruction

Indeed at the present moment this seems to be the outstanding need in the field of college instruction in landscape gardening. Ideals need to be clarified.

[4] Waugh, F. A. American Ideals in Landscape Architecture. Land. Arch. **15**: 151. Boston, 1925.
[5] The writer has prepared a text-book for this particular form of instruction: "Textbook of Landscape Gardening," Wiley, New York, 1923.

And especially is it imperative that a clear differentiation be made between professional and cultural (non-professional) courses.

In the agricultural colleges themselves, where, as we have seen, the urge for courses in landscape gardening is notably strong, there is a visible tendency to over-professionalize the instruction. This tendency is manifest in 3 specific symptoms:

1. Very early in the development of courses, sometimes from the outset, there is made a direct effort to turn out professional landscape gardeners. It seems altogether clear at the present time that the standards for professional training ought to be set much higher.

2. These higher standards being recognized, the effort to meet them, through the employment of more instructors and the multiplication of courses, is put forth by some institutions which might better be content with non-professional courses.

3. Even when misleading ambition points to neither one of these plans the one or two modest courses in landscape gardening are made altogether too "practical." Problems in home grounds design and school grounds design (favorite obsessions!) are attacked almost at the beginning. It would be much better to introduce these non-professional pupils to the simple principles of order and design, to the significant relations existing between landscape gardening and the other arts, and to give them some clue to an understanding of the vastly beautiful and omnipresent native landscape.

Professional Schools

The prevailing urge toward the establishment of new professional schools in landscape gardening has already been noted, and the opinion has been insinuated that more schools are not needed so much as higher stardards. To anyone in close touch with the work now being done this call for higher standards will appeal most strongly.

Harvard University School of Landscape Architecture maintains a 3-year professional graduate course. The work has now been divided into 2 courses, one dealing with general landscape architecture, the second with city planning, which latter subject is included in all ambitious curricula in landscape architecture. Now it is well recognized, especially by the instructors in Harvard, that the graduates of this intensive, extensive, 3-year graduate course are not too well prepared for the intricate and multifarious demands made upon a practicing landscape architect. Such graduates are nearly always sent to serve what amounts to an apprenticeship with established firms before they are thought competent to undertake independent practice.

In practically all of the other schools now active in this field the professional course is made a part of the baccalaureate curriculum. When the pupil finishes his 4 years and gets his bachelor's degree he is through with his formal study and is a professional landscape architect—as far as his college can make him. In these 4-year courses much has to be done besides landscape gardening. General

education in science, mathematics, language, history, economics and social sciences is usually a primary objective,—an objective so important that no professional training whatever should ever be permitted to supplant it. The most that can ever be done justly in a 4-year course is to combine a certain amount of professional training with a reasonable minimum of general education.

It is possible to speak more precisely, however, on this important point. It is customary, for example, to place the bulk of the general studies in the first 2 years and to allot a considerable part of the last 2 years to professional study. Expressed in units of college credit we may say that, in a 4-year course of 120 credits, at least 60 should be reserved for general studies; that not much more than 30 credits may be safely given to landscape gardening, with the remaining 30 free for collateral studies such as architecture, engineering, and horticulture.

Experience indicates once more that in all schools where such professional instruction is maintained the pressure is constant and heavy for a larger percentage of purely technical courses in landscape gardening. In short, the same tendency toward over-professionalizing the work operates with undiminished intensity.

It is the mature opinion of the present writer that this demand should be resisted; that courses on the 4-year basis should not permit the professional objective to set aside or surpass the cultural objectives of general education; that it is necessary in all cases to plan for a period of apprenticeship in the field after graduation; and finally that the most promising men should be urged to spend from 1 to 3 years in post graduate schools and in travel before remitting their formal training.

At the present time it is possible with some confidence to state 2 important unmet needs in this field of professional instruction in landscape architecture.

The first is for 2 or 3 first-class graduate schools with standards at least equal to those now maintained at Harvard. The country and the art of landscape architecture would be best served if one of these graduate schools could be founded at some strong university in the middle west, one on the Pacific Cost, and one in the South.

The second serious need is for a well-developed and generally recognized system of apprenticeship wherein men graduating from the various 4-year curricula (possibly from the graduate schools) could be assured of good discipline and sound training during their first few years out of college. Such a system would of course require the wide cooperation of employers. Perhaps it could be realized through joint action of several colleges on one side and the American Society of Landscape Architects on the other. At any rate, here is a real need which has not yet been met.

The foregoing criticism by no means covers every aspect of the subject. It is intended only to present some of the salient features of actual problems in the teaching of landscape gardening. It seems at least worth while to call attention to the very striking growth of this subject, largely out of the field of horticulture, and to suggest that these phenomena are highly significant of the changes taking place in the entire field of agriculture, horticulture, and the plant sciences.

FRUIT SPUR COMPOSITION IN RELATION TO FRUIT BUD FORMATION[1]

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During recent years professional horticulturists have found a new method of attack upon their problems in the study of the internal composition of the plants with which they work. This method has been adopted at the New Hampshire Experiment Station in carrying on the studies of fruit bud formation in the apple, which have been in progress there for a number of years. This method has been of particular interest since the investigations of Kraus and Kraybill ('18) on flower production and vegetation in the tomato and is one in which a number of investigators have recently made contributions.

It is to be hoped that the relation of composition to fruit bud formation may be established more easily than the relation of environmental factors, since the latter should find their expression in changed composition. This should lead to a more exact knowledge of the effect of various treatments on fruitfulness.

That differences in composition related to differences in fruit spur performance do exist has been shown by the results of several studies. Harvey ('23) found that the results of ringing and defoliation could be interpreted on the basis of the changes resulting in the relationship of carbohydrates to nitrogen, but that, in any given kind of material great differences in performance were correlated with rather small difference in this relation.

Hooker ('20) has found that alternate bearing spurs go through a two-year cycle of chemical changes and that their performance is correlated with the relationship of starch to nitrogen particularly at the time when fruit buds are being formed. He (Hooker '25) has also presented evidence which indicates that, under some conditions, an alternate bearing tree may be changed to an annual bearer by the application of nitrogen at the proper season.

At the New Hampshire Agricultural Experiment Station (Kraybill, et al. '25) it has been found that the differences in composition between bearing and non-bearing spurs of trees from the same plot are large compared with the differences between successive samples from the same plot. The relationship between carbohyrates and nitrogen is correlated with the behavior of the spurs. If, however, two plots of trees receiving widely different cultural treatments are compared, this correlation does not appear. Bearing spurs from a sod plot were almost exactly similar in starch accumulation and nitrogen content to non-bearing spurs from

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[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 18, 1926.

a cultivated plot receiving annual applications of nitrogen. The bearing spurs formed no fruit buds, the non-bearing spurs formed them abundantly.

As far as these studies have gone, it appears that performance and composition of fruit spurs are related, but that the relationships so far found are by no means exact, and hold for very uniform material. Thus nothing has been found that gives the analysis of fruit spurs or other parts of the tree practical diagnostic value.

Hooker ('20) has found that the relationships are more clear cut when starch alone is considered rather than total carbohydrates, and Nightingale ('22) working with other plants has found that insoluble nitrogen is more definitely correlated with performance than is total nitrogen. It is difficult to understand how the accumulation of insoluble substances can affect directly the type of development of the differentiating tissue. If correlation between fruit bud formation and the accumulation of these substances exists, it would seem that they must be parallel results of a common cause. Search for this common cause is an important task for the future and it is uncertain whether our present methods are adequate.

Of course, in any investigation the choice of material and methods is of the greatest importance, and the choice made by different workers will differ depending on the point of view from which the problem is attacked. Very often the difficulties met are so many and so conflicting that it is necessary to choose what appears under the circumstances to be the least of a number of evils. The problem under consideration is beset with a large number of these experimental difficulties, so it may be worth while to discuss a few of these briefly and to indicate the choice that has been made in the work now in progress.

It has been suggested that spur composition is dependent upon the composition of the wood and bark of the tree as a whole, and that a comprehensive study must include samples of these parts in addition to the spurs. Harvey and Murneek ('21) concluded that there is a considerable degree of individuality in the spurs they studied, amounting as far as fruit bud formation is concerned, to about 50 per cent of their normal function. Hooker and Bradford ('21) found that the unit sphere of influence affecting fruit bud formation, or correlated with it, may be the spur, the branch, or the whole tree in different cases. Even when spurs show marked individuality in their behavior it is undoubtedly true that extreme variations in the condition of the tree as a whole would influence spur performance. However, it would seem that at the time when differentiation is occuring, the conditions determining the course of development of a given bud must be largely local. It is the object of the present studies to try to learn what these conditions are. If this can be done it will be desirable later to find out how these in turn are affected by the conditions prevailing in more remote parts of the tree, and finally to trace them still further to the controlling environmental factors. For this reason the work at the New Hampshire Station has been limited to the spurs.

The meristematic region at the tip of the spur from which the embryo flowers develop is microscopic in size. It is entirely impractical to limit the chemical

sample to this tissue. How large a portion of the spur should be included is difficult to determine, because we know little about the degree to which nutrients may be localized at the tip or in different tissues. The work of Proebsting ('25) and of Tufts ('25) has shown that in apple shoots the composition of bark and wood may be very different. Harley ('25), taking samples of Stayman in June at the Maryland Station, found that the new growth of the spurs contained larger and more uniform quantities of carbohydrates than the older wood. His work would seem to indicate that results of analysis of spur samples containing growth older than one year would be unreliable, yet a large number of samples of Baldwin spurs including wood from one to three years of age, analyzed in the New Hampshire work show good uniformity of composition in successive samples of the same type of spurs taken at frequent intervals during the period from late June to August. Gardner ('25) has observed carbohydrate deposition taking place beginning at the tip of shoots at about the same time length growth ceases and proceeding downward or backward from the tip as the season progressed. This would lead us to expect that spur samples containing old growth would be least uniform early in the season. Harley's most uniform samples were from spurs of the same length of new growth. This would be expected because spurs of the same length would tend to cease growth at about the same time, and therefore would be in about the same stage as regards storage of nutrients.

Without doubt, the more nearly one can approach sampling the tip bud only, the better. However, other difficulties are met which force the choice in the other direction. In order to make determinations of the desirable number of constituents the fresh weight of the individual sample should be not much less than 25 gms. and a very large number of tip buds would be required to make a sample of this size.

The matter of estimating the performance of the spurs sampled offers many difficulties. Some investigators have sampled separately bearing and non-bearing spurs, knowing that the latter will form more flowers than the former, and assuming that any chemical differences found may be considered to be related to flower formation. We found, by counts made this spring, that last year's non-bearing spurs on Baldwin trees from different plots varied from 3 to 60 per cent in flower formation. Others have estimated performance by microscopical examination of a portion of the spurs sampled. This is a valuable method if one can be sure that differentiation is complete at the time the sample is taken. It is not applicable, however, to samples taken somewhat early in the season. We have attempted to meet this difficulty by sampling a definite type of spur and determining by actual count the following spring the performance of the spurs of that type remaining on the tree. In using this method it is necessary to remove few enough spurs from a tree so that their loss and that of their leaves may be assumed to have little or no influence on the performance of the remaining spurs of that type.

Counts of flower formation will reveal much variation between different trees, or, if the observations are carried farther, between different limbs or parts of the same tree. The larger the number of trees included the greater the range of variability in fruit bud production in the spurs used.

All the points just mentioned must influence the choice of the method of sampling. For our purpose we have tried to meet these difficulties by using only the current year's growth, thus avoiding the greater variability of composition of the older wood, confining the sample as nearly as possible to the parts most directly concerned, yet providing a sample of the required size from a reasonable number of spurs. For a single sample trees of the same age, in as nearly as possible the same condition, and all receiving the same cultural treatment were used. Five to nine trees were used for each sample, and the maximum number of spurs taken from one tree during the season was 200.

Only non-bearing spurs were used. It was assumed that non-bearing spurs from trees varying as widely in condition as those in the various plots of the Woodman and University orchards would show wide variations in performance. This assumption was shown to be correct by the counts made this spring. The disturbing effect of flower and fruit production was avoided by using only non-bearing spurs, and, since only the current year's growth was taken, no cluster bases were included.

While the time of flower differentiation has been studied microscopically to a considerable extent, more information would be desirable. The work of Goff ('01) on a number of apple varieties showed flowers on a few during June and July, on the largest proportion during August, and on some during September. Since he did not take a large number of buds at each date, it is possible that in a variety having a low percentage of flower buds these might not be found until the second or third sampling, even though present at the outset. The work of Kirby ('18) seems to indicate further, however, that while some flower primordia are formed in June, the majority do not appear until August. The season at which chemical differences in the spurs might be of importance is accordingly not conclusively demonstrated, and it may be that when we are comparing composition of spurs on two different plots, perhaps one cultivated and one in sod, the flowers in one case may be formed earlier than in the other. In our present work we have sampled twice; during the first week of July, and during the first week in August.

No doubt the exact methods used must vary with the point of attack on the problem, but it is hoped that adequate choice of methods combined with a more definite limitation of the immediate objective may bring out more clearly such relations between fruit spur composition and fruit bud formation as exist.

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SOME EFFECTS OF TEMPERATURE UPON THE RIPENING AND KEEPING OF FRUITS[1]

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An attempt is made in this paper to briefly summarize certain phases of work completed or under way at the University of California concerning the effects of temperature upon the ripening and keeping of fruits, and to interrelate certain portions with the work of other men.

Kidd and West ('25') have pointed out that when low non-freezing temperatures are used for the preservation of fresh fruit the general statement is made that the effect produced is simply one of slowing down the normal vital processes. They further point out that this generalization is not correct, that there is not only a retardation of the vital processes, but also a change in their character, which may lead to deleterious results in some cases.

Curtis ('26) has shown that temperature influences not only the rate of respiration but also the course or nature of the process.

The writer wishes to emphasize this idea that the course or character of metabolism as well as the rate, both in storage and in the field, may be modified by temperatures above and below the "normal or optimum" as recognized upon the basis of the usual or expected metabolic responses. Further, the generalizations concerning the "optimum" ripening or keeping temperatures for the fruits of even a single species of economic importance are unsafe. Indeed, it is difficult to determine the "optimum" temperature either for greatest retardation or maximum acceleration of the metabolic processes, since so much depends upon the previous environment of the product, the stage of development attained when harvested and stored, and the duration of the particular storage temperature.

The work reported, which it is believed indicates this to be true, may be grouped under topics as follows:

1. The apparent effect of high temperatures, in the field and in storage, upon the ripening of certain fruits.

2. Certain effects of relatively low growing-season temperatures upon the apple.

3. Certain effects of cold storage temperatures upon internal browning, soft scald, and scald, physiological diseases of the apple.

4. Some unusual ripening responses of fruits to low temperatures.

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 19, 1926.

Some Effects of High Temperatures upon the Ripening of Pears

Shamel ('17) reported that when hard ripe Bartlett pears were stored at relatively high temperatures ranging from 26° to 38°C., with the relative humidity varying from 85–96 per cent, they kept for about thirty days. Similar pears, however, kept at lower temperatures and humidities ripened within a week. Shamel attributed the retardation in ripening to the high humidities. Data by other workers, however (Overholser and Taylor '20), indicated that relatively high temperatures retarded ripening both in the field and after harvest, rather than high humidities.

The writer ('17) obtained evidence that certain varieties of plums and cherries doubly and trebly enclosed, early in their development, in closely woven black sateen cloth sacks were appreciably delayed in attainment of maturity and prolonged in period of edibility. Subsequent work (Overholser, Winkler, and Jacob '23) showed that when apples were enclosed in a single similar cloth sack the temperature of the fruits averaged approximately 8.5°C. higher than the air temperatures. The temperature in the sacks enclosing the plums and cherries must have averaged considerably higher than the air temperatures, and this may have delayed the ripening of the enclosed fruit. The carbon dioxide content of the air within the sacks and especially of the inter-cellular spaces (Magness '20) of the enclosed fruits must also have been increased. Coincidently the oxygen supply would have been reduced (Magness '20). This no doubt would also have retarded ripening since Kidd and West ('22) state that apples stored in tight containers until the oxygen in the air was reduced to from 5 to 8 per cent, and the carbon dioxide increased to 15 per cent by the respiration of the fruit, and this ratio then maintained by ventilation, kept twice as long as controls held in air. They report that to avoid injury to the fruit, the oxygen should not fall below 5 per cent and the carbon dioxide should not go above 15 per cent.

Kidd and West ('23) in another paper state that certain increased concentrations of carbon dioxide retarded the ripening of fruits without causing injury; though concentrations of carbon dioxide as high as 13.6 per cent of the atmosphere surrounding the fruit may cause serious injury.

The writer has found that the exclusion of oxygen from several varieties of Japanese plums (most work was done with the Climax) prevented the development of red or blue colors at any of the temperatures tested, both in the light and darkness, although the fruit gradually broke down from autolysis. The delay in the development of color by the trebly sacked plums, it would appear, may have resulted from oxygen deficiency rather than light exclusion.

Observations in California (Overholser and Taylor '20) indicated that excessively high summer temperatures may delay the attainment of maturity of Bartlett pears on the tree.

Bioletti ('15) believed that the high summer temperatures of some of the excessively hot southern interior valleys of California accounted for the later ripening of certain varieties of European grape (*Vitis vinifera L.*) as compared with those grown in valleys somewhat less hot further north.

The work reported from the University of California in 1920 (Overholser and Taylor) showed that storage temperatures of 31° to 43°C., especially 34° to 40°C., caused an appreciable delay in the ripening of pears, together with the development of abnormal flavors, as contrasted with the more rapid ripening at temperatures of 21° to 29 C.° This work has been subsequently repeated using Anjou, Hardy, and Comice with similar results. Temperatures of 50°C and above "baked" the pears and resulted in such profound changes that ripening could not be studied.

In attempting to account for this observed effect of high temperatures at the time the data were published the effect of the possible accumulation of carbon dioxide in the ripening chamber was recognized, but was not given much weight because of the adequacy of ventilation. The possible increase in the carbon dioxide content of the intercellular spaces of the fruit, at these high temperatures, notwithstanding this ventilation, was not recognized.

As a result of work subsequently published by Magness ('20), and Kidd and West ('23), together with the work of Kidd ('14), the possible accumulation of carbon dioxide and reduction of oxygen in the intercellular spaces of the fruit might be expected partially to account for the retarded ripening. Magness ('20), it will be recalled, analysed the gases in the intercellular spaces of Newtown apples and found that at 2°C. the proportion of carbon dioxide was relatively lower than that of oxygen, 6.7 per cent and 14.2 per cent respectively. At higher temperatures, however, the proportion of carbon dioxide to oxygen became much greater and at 30°C. was 21.4 to 3.2 per cent respectively. Kidd and West ('23) obtained similar results with the Bramley Seedling apple, although the increase in carbon dioxide at higher temperatures was less marked.

Kidd ('14) found that carbon dioxide depressed both anaerobic and aerobic carbon dioxide production. Quantitatively the degree of depression appeared to be proportional to the square root of the concentration of carbon dioxide over a range of 0–50 per cent carbon dioxide at one atmosphere pressure.

Under possible conditions of high temperatures reported for the sacked plums and cherries, Bartlett pears in the field, and pears stored after harvest, it is conceivable that the carbon dioxide content of the intercellular spaces may have been relatively high and the oxygen supply low, and that this indirect effect of the high temperatures may have retarded respiration and thus may have been partially responsible for the retarded ripening.

Respiration. A graduate student, of the University of California, de Villiers ('21), in attempting to find an explanation for the delay in the ripening of pears at the higher temperatures, studied their effect upon the respiratory intensity as measured by the carbon dioxide production. He used a method subsequently described by Bennett and Bartholomew ('24) with wide mouth five-liter glass jars as respiration chambers, containing from 700 to 800 gms. of fruit.

The fruits and jars were kept at each of the temperatures 12 to 24 hours, the fruits were then quickly placed in the jars, which were sealed with the stop cocks open, and replaced at the temperature desired for one hour, to permit constant temperature and pressure to be attained, when the stopcocks were closed

and the experiment begun. At the temperatures of 35° and 40°C. the interval employed was about 14 hours, and at the lower temperatures longer intervals of time were employed so that the carbon dioxide increase and oxygen decrease in the jars was more nearly the same at each temperature. Duplicate samples of gas of each of the jars were analyzed for carbon dioxide and oxygen content, and the respiration expressed in mgms. of carbon dioxide produced per kgm. of fruit per hour.

In table 1 are given some previously unpublished data obtained by de Villiers, which are the average of from three to five pickings of three varieties made June 21, August 18, 28, and September 8 and 17.

TABLE 1. THE AVERAGE EFFECT OF TEMPERATURE UPON THE RATE OF RESPIRATION OF HARDY, COMICE, AND BOSC PEARS

Temp. °C.	No. dupl. tests, average	Average sample, gms.	Dur. of exp., hours	Percentage of gases		Mgms. CO_2 per kgm. per hour	Respiratory ratio CO_2/O_2
				CO_2	O_2		
0°	14	703	168.4	2.57	16.20	2.13	.676
2.2°	11	844	166.8	3.83	15.14	2.23	.788
9.1°	11	877	63.0	4.56	14.87	6.97	.888
21.1°	23	731	35.6	5.92	11.56	18.85	.701
35.2°	10	721	13.3	6.66	11.30	57.30	.765
40.4	9	845	14.0	9.21	10.20	59.75	.938

It is of interest to note that the respiration ratio at the different temperatures tended to vary, being lowest at 0° and increasing up to and inclusive of 9.1°C. At 21.1°C. the respiration ratio reached a second minimum, with a further approach to unity at 35.2° and 40.4°C. This was true of the individual determinations as well as the averages. This may be accepted as indicating that the character of the respiration is affected as well as the rate.

These data indicated that the higher the temperature up to 40° C. the greater the respiratory intensity. It will be recalled, however, that at the temperatures of 35° and 40°C. the fruit was retained for a maximum of not over 38 hours, while the fruits used to demonstrate the retarding effect upon ripening were stored two weeks or more. Blackman's ('05) limiting and retarding factors probably would not have been exerted in the first case but probably would have in the second.

The writer later conducted further experiments upon respiration at the higher temperatures, with longer exposures. The procedure was similar to that described but after the first gas analysis, the jars were aerated by means of a suction pump and tubing for 8–10 hours until the carbon dioxide and oxygen contents of the jars were normal. The stopcocks were then closed and the respiration intensity

during this second period was determined. The tests were repeated during a succeeding interval of time. The data are given in Table 2.

TABLE 2. THE INHIBITING EFFECT OF MAXIMUM TEMPERATURES UPON RESPIRATION OF HARDY PEARS

Temp. °C	Weight sample (gms.)	Interval	Duration resp'n. exp., hrs.	% CO_2	% O_2	Mgms. CO_2 per kgm. per hour	Respiratory ratio CO_2/O_2
35.6°C	625	1st 24 hrs.	17.5	7.27	11.7	49.7	.87
35.6°C	625	2nd 24 hrs.	17.0	6.20	12.9	42.5	.87
35.6°C	625	3rd 24 hrs.	17.0	5.30	14.0	36.3	.88
42.1°C	1040	1st 24 hrs.	13.0	12.8	9.8	69.2	1.25
42.1°C	1040	2nd 24 hrs.	11.0	9.6	10.6	61.1	1.01
42.1°C	1040	3rd 24 hrs.	10.0	7.2	12.1	51.7	0.91
51.2°C	770	1st 24 hrs.	11.0	11.4	10.6	102.7	1.20
51.2°C	770	2nd 24 hrs.	13.0	1.4	19.4	11.0	2.33
51.2°C	770	3rd 24 hrs.	10.0	0.6	19.8	6.1	3.00

The data in tables 1 and 2 indicate that while with short exposures to high temperatures the respiration rate is increased, with longer exposures the rate very rapidly fell off at 51.2°C. and was checked appreciably after 72 hours at 42.1°C. and 35.6°C. These data further indicate that at the higher temperatures the metabolism is retarded.

In this connection it is of interest to refer to unpublished data by Hopkins ('26) who measured the carbon dioxide production by an absorption method of individual potato tubers for five consecutive 48-hour periods at 25°C. With one set of Cobbler potatoes the average production of carbon dioxide per tuber (using ten tubers) for the first 48 hours was 15.73 mgms. per kgm. per hour and for the fifth period 12.71. With a second set of ten tubers, which had been stored for a time at 10°C. and then kept at 25°C. for the respiration studies, the average production per tuber of carbon dioxide during the first 48 hours was 30.66 mgms. per kgm. per hour and for the fifth 9.91. Hopkins believes these data definitely show a slowing up of respiration and he suggests that since in all cases the tubers had been previously stored at a temperature lower than 25°C., this rise in temperature at first resulted in an increase in respiration, the increase being more marked the greater the relative temperature rise. At the higher temperatures, however, Hopkins suggests there was a change from sugar to starch and this decreased the amount of sugar available for respiration. Sugar was also being used in respiration, and thus respiration was diminished.

Pectosinase. de Villiers ('21) devoted further study to the effect of high temperatures in retarding ripening. While it is recognized that as fleshy fruits ripen there appears to be at least a partial dissolution of the middle lamella and separation of the cells from one another, the exact nature of middle lamella and the cause of the weakening of the cells as the fruit becomes overripe is not known. Carrick ('24) has suggested it is possible that the calcium salts of pectic acid in the middle lamella may be hydrolyzed by an increased hydrogen-ion concen-

tration, or by an enzyme such as pectase, (designated by Atkins ('16) as pecto-
sinase, and by others as pectinase) into soluble compounds which no longer
cause the cell walls to adhere firmly to one another.

Since the pears at the higher temperatures remained firm in texture, he rasied
the question as to whether the activity of this enzyme might not have been re-
tarded. Employing methods of Ehrlich ('17) he found that the amounts of cal-
cium-magnesium pectate in comparable samples of pears stored for seven days
at 0°, 20°, and 42–44°C. was about the same for fruits stored at 0° and at 42–44°C.,
but at 20°C. the amount was about 16 per cent less.

It was concluded by de Villiers that the dissolution of the cementing matter
of the cell walls was more rapid at room temperatures than at 0° and 42°C., and
that this lessened activity of the enzyme involved may partly account for the
retarded ripening. He, however, did not repeat the work, and it is possible that
his methods may have been unsatisfactory.

CERTAIN EFFECTS OF RELATIVELY LOW GROWING SEASON TEMPERATURES UPON APPLE FRUITS

The observations of Ballard, Magness, and Hawkins ('22) indicated that
internal browning was serious only in apples from the floor of the Pajaro Valley
where the temperatures of the growing season were relatively cool, While some
internal browning occurred in fruit from the orchards on the hills above the fog
belts, it was not commercially serious in such districts, where the temperatures
during the growing season were higher.

Work at the University of California (Winkler '23, and Overholser, Winkler,
and Jacob '23) showed a relation between orchard temperatures during the grow-
ing season and the subsequent development of internal browning of the New-
town apple in cold storage.

A study of the temperature records for the Pajaro Valley, where the New-
town is grown in California, indicates that in 1908 and 1914, years in which
heavy losses from internal browning occurred, the mean temperature from June
to September was low. For 1915 and 1916, when the mean temperature for these
months of the growing season was nearer the normal, the severity of the brown-
ing was also less. In 1912, 1913, 1917, and 1918, years of higher mean temper-
atures for the same months, little or no internal browning developed.

A comparison of the temperature records of the Pajaro Valley with those of
two other localities where the Newtown is commercially grown further empha-
sized the relation of internal browning to growing season temperatures. Compar-
ing the temperature records of the Pajaro Valley with those of Rogue River
Valley, Oregon, and Albermarle County, Virginia, it was found that the mean
temperature of the growing season was about 3°C. and 7°C. higher, respectively,
than that of the Pajaro Valley.

EFFECT OF ARTIFICIAL MODIFICATION OF TEMPERATURE OF FRUIT IN THE ORCHARD

During each of the seasons of 1920 and 1921, the fruits of a single tree were
kept at temperatures lower than that of normally exposed fruits, by means of

shading effected by large tents. During the growing season of the two years, several hundred fruits, distributed at random over ten trees, were enclosed in black cloth bags, at temperatures higher than those normally exposed.

The fruits under the tent, as a result of the exclusion of direct sunlight, had a temperature about 5.3°C. lower than normally exposed fruits. When the sun was shining the normally exposed fruits outside the tent had an average temperature of about 4.0°C. higher than air temperature, as a result of heat absorption during periods of sunshine. Regardless of the treatment given on foggy days, the fruit, not tented, approached the temperature of the open air. The daily mean temperature at the core of the fruit in black bags was about 5.6°C. higher than that of apples normally exposed.

The bagged fruit and checks from similar positions on the same trees, together with fruit from the tented tree and the fruit from two adjacent trees for checks, were all harvested at the same time and stored under identical conditions at 0°C. As the bagged, tented, and check fruit behaved similarly, only the averages for all the lots are given in table 3.

TABLE 3. EFFECT OF ORCHARD TEMPERATURE UPON INTERNAL BROWNING

Treatment	Average temperature, sun	Average temperature, shade	Average temperature, foggy days	Per cent normal
Apples in black bags	31.2°C.	22.3°C.	19.5°C.	84
Normally exposed apples	26.0°C.	19.0°C.	17.3°C.	28
Apples in shade of tent	20.7°C.*			20
Air temperature	22.0°C.	18.0°C.	16.2°C.	

* Average temperature throughout growing season.

These data indicated a definite relationship between the orchard temperature and internal browning. Temperatures of about 5°C. above that of the normally exposed fruit reduced the browning, and temperatures about 4°C. below that of normally exposed fruit increased the browning.

EFFECT OF EXPOSURE UPON TREE

Results which confirmed this relation of orchard temperature to browning were obtained by collecting fruit from well exposed and shaded portions of the tree. During the seasons of 1920 and 1921, fruit was collected from the upper southwest periphery of two trees, where the fruit received the maximum effect of the sun's rays, and also from the lower north part of the same trees where the fruit was continuously in the shade, and stored under identical conditions at 0°C. The results are given in table 4.

These data show nearly twice as much browning in fruit from the same trees when picked from the shaded portions as contrasted with the exposed portions. Temperature records show that during the day the temperature of the well exposed fruit averaged over 7°C. higher than that from the shaded side of the tree.

Since the work in California was reported, Adam ('24) in Australia found that Rokewood apples grown in the north of Victoria, where the climate is warm,

TABLE 4. EFFECT OF EXPOSURE OF FRUIT UPON INTERNAL BROWNING

Position of fruit on trees	Average fruit temperature during day	The percentage of fruits showing the various degrees of browning				
		normal	trace	slight	mod.	severe
Well exposed on S. W. periphery of tree	26.7°C.	42	44	11	3	0
Shaded interior N. side of tree	19.5°C.	22	43	22	12	1

developed little internal browning, as compared with apples of the same variety from Gippsland, where the climate is colder. The apples from both localities received similar treatment during the storage trials.

THE EFFECT OF STORAGE TEMPERATURE UPON INTERNAL BROWNING

Investigations by Powell and Fulton ('03) indicated that all apples could be best stored at about 0°C. Losses, however, were incurred through internal browning of Pajaro Valley grown Newtown apples when stored at this temperature. Through the work of Stubenrauch ('10) Pajaro Valley apples have been stored at 2.0°C since about 1910. Ballard, et al., ('22) stated that browning can be largely prevented by storing Pajaro Valley apples at 2.0°C.–3.3°C.

In the experiments at the University of California, apples from the Pajaro Valley were stored at 0°C and 2.0°C for five seasons and it was found that considerable browning occured after February 1, even in the fruit stored at 2.0°C. Apples were, therefore, stored at various degrees of temperature above 2.0°C to determine the lowest temperature at which internal browning would not develop during an average storage period.

The averages, after five months storage each season, for all the lots at each of the temperatures employed are recorded in table 5.

TABLE 5. EFFECT OF STORAGE TEMPERATURE UPON INTERNAL BROWNING

Storage temperature	The percentage of fruits showing various degrees of browning				
	normal	trace	slight	moderate	severe
− 1.1°C.	10	26	24	25	15
0.0°C.	15	25	21	25	14
2.2°C.	35	37	16	9	3
4.5°C.	74	23	3	0	0
7.0°C.	95	5	0	0	0
14.0°C.	100	0	0	0	0
21.0°C.	100	0	0	0	0

The results obtained showed a definite relation between the amount of internal browning and the storage temperature. Browning did not occur in any of the fruit stored at a temperature of 14.0°C or above.

Almost no browning occurred at 7.0°C. and the fruit remained marketable when stored at 4.5°, in that "trace browning" was not considered sufficient to lessen the market value of the fruit.

The browning was not only increased in severity as the temperature decreased below 4.5°C, but its development was also more rapid. The apples stored at 0° showed browning a month prior to its detection in the fruit stored at 2.2°, and the apples held at 4.5° remained normal for almost two months after those stored at 2.0°C. had begun to brown.

Kidd and West ('25a) in storage trials with three varieties of English apples showed clearly that internal browning (internal breakdown) occurred earlier and to a more serious extent when the fruit was stored at 0°C. than when stored at 3°C., 8°C., and 12°C.

It is interesting to note that in England, where the temperatures of the growing season are comparatively low, internal browning appears to be a trouble affecting several varieties.

Soft scald in the Jonathan variety was also found by Carrick ('26) to be markedly favored by −1.5°C. and prompt storage. This substantiates the work of Magness and Burroughs ('23) and of Plagge ('25) to the effect that while soft scald developed at 0°C. it did not occur at temperatures of 2°C. and above.

As opposed to the possible injurious effects of low storage temperatures upon internal browning and soft scald Carrick ('24) reported that the development of apple scald in the Wagener variety was much less rapid while stored at 1.0°C. as compared with 0° or 2.0°. This is in agreement with the extensive work of Brooks, Cooley, and Fisher ('23), although these workers did not use a temperature below 0°C.

In later work, Carrick (unpublished, '26) found this same relationship in the Rhode Island Greening and Baldwin when held at −1.5°C. Even after the fruit had been exposed for several days at room temperature, scald was seldom as severe in the apples kept at −1.5°C. However, it was repeatedly observed that a type of browning which the present writer considers comparable to internal browning developed around the carpels in R. I. Greening, McIntosh, and Baldwin much sooner at −1.5°C. than at 0°. The discoloration occurred in storage, but rapidly increased when the fruit was withdrawn to 20°C. This breakdown seemed to be favored by either early or late pickings and was reduced by a delay of several days after harvest before storage.

Certain Unusual Ripening Responses of Fruits to Low Cold Storage Temperatures

Pears. The work of Lewis, Magness, and Cate ('18) and Lewis, Murneek, and Cate ('19) indicated that the flavor of the Bosc was influenced by the ripening temperature. They found that this fruit did not reach maximum flavor in cold storage, and that it was necessary for a part of its ripening process to take place at a temperature as high as 16°C.

Work reported from the University of California (Overholser and Latimer '24) indicated that certain varieties of pears, particularly Bosc, but also the Howell, Forelle, Gray Winter, and Vicar, when picked in a relatively immature condition, kept and ripened better at 2.2°C. than at −1.0°. When picked too immaturely the Bosc did not ripen properly at −1.0°C. The fruit either de-

veloped a soft rot about the core, or wilted and remained fairly firm, and became insipid in flavor. At 2.0°C., however, similar specimens of Bosc gradually ripened and remained in a marketable condition, except for slight wilting, for a longer period of time.

When immature pears were stored at −1.0°C. each week seemed to accentuate slight variations in the original degree of ripeness, seemingly because of unequal disturbances of the various ripening processes over a relatively long period of time. The Louise variety, for example, picked in a somewhat immature condition, ripened fairly satisfactorily both at room temperature (18°–24°C.) and at a temperature of 2.0°, but toward the end of its storage period at −1.0°C., in late November and early December, the lots when removed exhibited various stages of ripeness from a yellow blush, medium soft ripe, to a grass green, hard, unripe condition.

Avocados. The published observations as to the best storage temperature for avocados are not entirely in agreement. Dybowski ('02) reported that 2.0°C. was the most satisfactory storage temperature. Wilcox ('14) reported that avocados could be held without injury to the fruit at 0°, for at least two months. Condit ('15) stated that avocados could be held for two months at temperatures of from 0° to 2°C. Higgins, Hunn, and Holt ('11) reported that prolonged storage temperatures of 0° to 2°C. resulted in the blackening of the interior of the avocado although such temperatures could apparently be endured without injury for about three or four weeks. They recommended that the temperature should not be permitted to fall below 4.5°.

Work reported from the University of California (Overholser '25) indicated that 0°C. was too low a temperature for the successful storage of most varieties of avocados. At this low temperature, the skin tended to exhibit a scalded appearance, the flesh remained firm but turned brown, and upon removal the fruit subsequently failed to ripen and soften properly. Ten varieties of avocados were stored at temperatures of 0°, 2.0°, 4.5°, 7.0°, and 18° to 24°C. during one to three seasons. The optimum storage temperature and the maximum keeping period for avocados picked in a hard, mature stage, are given in table 6.

TABLE 6. THE AVERAGE KEEPING QUALITY OF CERTAIN AVOCADOS
AT THEIR OPTIMUM TEMPERATURE

Variety	Average date stored		Year of tests	Optimum storage temperature	Period of maximum storage (days)
Dickinson	July	4	1921	4.5°C.	68
Royal	March	7	1920	0.0°C.	60
Taft	July	4	1924	4.5°C.	56
Queen	July	8	1921	4.5°C.	54
Spinks	May	19	1920, 21, 24	4.5°C.	47
Sharpless	Nov.	22	1921	4.5°C.	41
Challenge	March	7	1920	2.0°C.*	40
Rey	June	9	1920	2.0°C.*	31
Fuerte	March	11	1920, 21	7.0°C.	30
Kist	June	9	1920	2.0°C.*	26

* Temperature of 4.5°C. not employed.

Most varieties kept best at a temperature of 4.5°C., the fruit ripening satis-factorily in storage or subsequent to removal and attaining good quality. Fur-thermore, 4. 5° sufficiently retarded ripening to prolong appreciably the market-ing period.

The observations of one year indicated that the Royal avocado may be an exception, in that under certain conditions it apparently may be kept satis-factorily at 0°C. The Fuerte, also, during two seasons proved to be an exception in that at temperatures below 7.0° the normally green skin tended to blacken, with some darkening of the flesh, especially about the vascular strands of the basal end. For the Challenge, Rey, and Kist varieties, studied only one year 2.0° is given as the optimum temperature, as contrasted to 0° and 7.0°, but a temperature of 4.5°C. was not employed for these varieties.

Summary and Conclusions

1. The writer has emphasized the idea that with fruits the *course* or character of metabolism as well as the *rate*, both in storage and in the field, may be modified by temperatures above and below the so-called "normal" or "optimum" temper-ature.

2. It is also pointed out that it is difficult if not impossible to determine the "optimum" temperature for either greatest retardation or maximum ac-celeration of the metabolic processes of fruits.

3. In support of these ideas certain published and unpublished works are cited as follows:

(a) The enclosing of cherries and plums in three closely woven black cloth sacks delayed ripening and color production, possibly by increasing the temper-ature and carbon dioxide content of the intercellular spaces, and by reducing the oxygen supply.

(b) High temperatures in the field and in storage (31° to 43°C.) retarded the ripening of pears as contrasted to temperatures of 21° to 29°C.

(c) While de Villiers found with pears for short periods of exposure (not over 38 hours) at temperatures of 35° and 40°C. greatly increased respiration, the writer found that longer exposures of 72 hours greatly retarded respiration.

(d) de Villiers also appeared to find that at temperatures of 0° and 42–44°C. the activity of the enzyme pectase (pectosinase, pectinase) was reduced as con-trasted with the activity at 20°C.

(e) Growing season temperatures which averaged 3° to 7°C. lower than more nearly optimum mean temperatures resulted in increased subsequent suscept-ibility of the Yellow Newtown to internal browning in storage.

(f) When these temperatures of the fruit during the growing season were artificially modified by shading (enclosing in black bags or picking with reference to exposure upon the tree) an increase in temperature diminished internal brown-ing and a decrease favored its development.

(g) Internal browning and soft scald developed earlier in the season and with greater severity when the fruit was stored at 0°C. than when stored at 7° and

above. Scald development is retarded, however, by temperatures of 0° or slightly below, as contrasted with storage at higher temperatures.

(h) When picked in a somewhat immature condition several varieties of pears did not ripen or attain satisfactory quality when stored at 0°, but did when stored at 2.0°C.

(i) Most varieties of avocados appeared to keep most satisfactorily at temperatures of 4.5°C. At lower temperatures discoloration of the epidermis, or flesh, and subsequent failure to ripen resulted; while at the higher temperatures, overripeness, molds, and general decay followed too rapidly.

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STUDIES IN THE NUTRITION OF FRUIT TREES[1]

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In the past a very large number of field experiments have been carried out with a view to ascertaining the effects of various systems of manuring on the growth and fruiting characters of the different fruit plants under cultivation.

In considering the accounts of these experiments one is struck by the conflicting nature of the results obtained in the different experiments and by the relatively small amount of knowledge which has been gained from them. Perhaps the one definite point which has emerged is that nitrogen, applied in the form of quickly available fertilisers, such as nitrate of soda and sulphate of ammonia, may be relied upon to increase yields in the tree fruits in cases where the trees are low in vigor, as is usually the case when they are grown under sod for any considerable period.

The parts played by phosphorus and potassium in the growth and fruiting processes of fruit trees are but little understood as the results obtained in the field, hitherto, from the use of phosphatic and potassic fertilisers have been very indefinite in character.

In view of such results, when a programme of work on the nutrition of fruit trees was considered by workers at the Long Ashton Research Station, it was thought that a better understanding of the problems might be gained by carrying out carefully controlled pot experiments previous to proceeding with any extensive programme of field work, and this method of approaching the problem was accordingly adopted.

It is the purpose of the present paper to give some account of the results which have been obtained in experiments of this type which have been carried out during the period 1920-1925.

Detailed accounts of the experiments have been published previously by the reader in two papers[2] and, as the time available for the present paper will not allow of a full account of the work being given, I propose to present here a brief summary of the main results obtained and would refer anyone interested in the details of the experiments to the above papers.

AIMS OF THE EXPERIMENTS

The specific problems which the experiments were designed to study may be stated as follows:--

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 17, 1926.

[2] Wallace, T. Experiments on the manuring of fruit trees. Journal of Pomology and Horticultural Science (England). 4: (3, 4); June, 1925; 5: (1); Dec., 1925.

1. How are the processes of growth, fruiting, etc. of the various fruit trees, bushes and plants affected when they are starved with respect to any one of the following essential elements of plant food,—nitrogen, potassium, phosphorus, calcium, magnesium, sulphur?

2. How do such plants react to different ratios of these elements in the nutrient media?

3. How do these plants behave in nutrient media containing all of the above elements but of widely differing reactions?

Materials and Methods

Apple trees, gooseberry and black currant bushes and raspberry and strawberry plants were used in the experiments. They were grown in quartz sand of which approximately 99.5% was insoluble in boiling hydrochloric acid. The sand was contained in unglazed but previously waxed 10-inch earthenware pots—10 kilos of dry sand per pot—in all cases except with strawberries, where 6-inch pots —2.5 kilos. of dry sand per pot—were used.

In the cases of apples, gooseberries and black currants the plants were grown under open-air conditions in a cage whilst the raspberry and strawberry plants were grown under a glass-roofed open-sided shed. Rain was prevented from gaining access to the sand in the pots placed in the cage by fitting stout tarpaulin covers over the mouths of the pots.

The various nutrients were supplied to the plants by means of nutrient solutions which were applied in such quantities to maintain the moisture contents at approximately 20 per cent of the weights of the dry sand. Accumulation of salts was avoided by periodic leaching of the sand with water.

The water used was rain water which was collected from the roofs of greenhouses. Periodic determinations of the composition of the water were made.

The composition of the complete nutrient solution used is as given below:–

	gms.
Sodium nitrate	5.0
Potassium nitrate	2.0
Di-potassium mono-hydrogen phosphate	1.0
Calcium sulphate, anhydrous	1.0
Magnesium sulphate 7 H_2O	1.0
Sodium chloride	1.0
Ferric chloride	0.4
Rain water	to 1 liter.

This solution was further diluted with rain water in the proportion of 1 liter of solution to 9 liters of rain water previous to application.

To obtain solutions deficient in any one of the various elements the following procedure was adopted: When it was desired to omit a base-forming element such as potassium, equivalent amounts of sodium salts were substituted in the complete solution vice the potassium salts; where nitrogen or phosphorus was omitted nitrates or phosphates were replaced by equivalent amounts of sulphates, and where sulphur was omitted chlorides were substituted for sulphates.

The complete solution was found to be well suited for the work except in the case of the experiments with apple trees where it was found necessary during the course of the work to increase the amounts of potassium and magnesium in the solution.

The apple trees used were two year old trees—the majority of which were on Malling Type I stock, the remainder being on "free" stocks. Previous to planting, all trees were root pruned in the Stringfellow method and the shoots were given a normal winter pruning. Black currants were two year old plants and at planting the fiber was removed from the roots and the shoots were cut off near their bases. Two year old gooseberry plants were used and at planting the fibrous roots were removed and the shoots pruned back close to the main stem. The raspberry material planted consisted of vigorous young canes. At planting the fiber was removed from the roots and the canes were cut down to near the level of the sand.

Vigorous young strawberry runners were used. These were planted without any trimming of roots or tops.

I. Deficiency Experiments

In these experiments the various plants were grown under the following treatments: (1) Complete nutrient solution; (2) nitrogen omitted; (3) potassium omitted; (4) phosphorus omitted; (5) calcium omitted; (6) magnesium omitted; (7) sulphur omitted; (8) water only.

RESULTS

As the results obtained on the various kinds of plants for any one treatment were generally similar I shall give a summarised account of the main results obtained from the various treatments and only deal in detail with those points which are of special interest.

In presenting the results of these experiments in the two papers previously referred to, numerous illustrations and tables of quantitative data are given. On this occasion I propose to bring to your notice only a few of the latter in illustration of the more salient points of the results.

In every experiment data were obtained on the following points: (a) Times of opening of leaf and blossom buds; (b) blossom characters; (c) Foliage characters throughout the season; (d) shoot growth; (e) defoliation,—time of of defoliation and tints; (f) conditions of barks of trees; (g) yields and characters of fruits; and (h) root systems.

COMPLETE NUTRIENT SOLUTION

Under this treatment all the plants made excellent growth. They blossomed strongly, made good shoot growth, bore foliage of normal character, matured crops of normal fruits, and developed good root systems.

In the following descriptions of the behavior of the plants receiving the various deficiency treatments, their performances are described in relation to those of the above series.

OMISSION OF NITROGEN

The effects produced by the omission of nitrogen were more striking than from the omission of any other element. In fact, the plants receiving this treatment differed very little as regards growth and extent of fruiting, etc. from those receiving water only.

The times of opening of the blossom and leaf buds were delayed, blossom formation was greatly reduced, and the flowers were extremely weak. The foliage was very scanty and after a season or two of the treatment the plants usually carried foliage only at the tips of shoots. The leaves were small and pale green in color and generally became yellowish green as the season advanced. Shoot growth was much reduced and apple trees, after two or three seasons under the treatment, were unable to make more than a few millimeters of growth during the season. The number of crowns produced by strawberry plants was relatively small. Defoliation was hastened to a considerable extent, and the tints developed during defoliation were reddish yellow. The barks of trees were pale brown in color. Fruit production was reduced more by this treatment than by any other, as all lateral buds along the shoots died. Apples produced in this series were small and highly colored, being similar to fruits produced on trees of low vigor growing under sod.

The root systems were small and in proportion to the shoot portions of the plants and consisted almost wholly of fine fibrous material.

TABLE 1. BLOSSOM COUNTS ON APPLE TREES, SEASON 1923—THIRD SEASON OF TREATMENT SHOWING NUMBERS OF BLOSSOM TRUSSES.

Treatment	Tree No. 1.	2.	3.	4.	5.	Totals
Complete nutrient solution	33*	46	34	30	22	165
Nitrogen omitted	19*	4	0	1	0	24
Potassium omitted	16*	32	19	23	21	111
Phosphorus omitted	5*	20	13	3	2	43
Calcium omitted	42	41	20	30	32	165
Magnesium omitted	50	40	36	13	8	147
Water only	29*	3	0	2	1	35

* Denotes "free" stocks; all other trees were on Malling No. 1. stock.

OMISSION OF POTASSIUM

The omission of this element did not produce such marked effects as those resulting from the omission of nitrogen. Blossom and leaf buds opened normally in the spring and the number of blossom buds was not reduced to any significant extent. The blossoms were strong and normal in every way. During the early part of each season the foliage characters were normal, and it was not possible to distinguish between leaves in this series and those in the series receiving the complete nutrient solution. Towards the end of May and in early June, special symptoms usually appeared. The color of the leaves became slightly bluish green and the leaves showed a tendency to curl backwards towards the under surfaces. They were also usually slightly reduced in size at this stage. Pale

markings appeared around their margins and later in the season these marginal areas became brown due to the death of the cells in those areas.[3]   In the case of raspberry leaves, the browning generally extended inwards from the marginal areas between the veins towards the midribs.   The above conditions generally developed rapidly under conditions of bright sunshine following cool spring weather favorable to the development of the foliage. Shoot growth was usually somewhat reduced and it was observed that plants under this treatment usually made excellent growth in spring and often good growth during autumn, but that during the warm months of summer shoot growth was often exceedingly poor. This was most noticeable in the case of raspberries.   Defoliation frequently occurred prematurely during the summer following the development of marginal leaf scorch, but it was evident that defoliation in such cases was not due to a cessation of growth activities for the season, as affected trees often developed a second set of foliage and continued to hold the latter as long into the autumn as did trees receiving the complete nutrient solution. During defoliation the leaves often turned direct from green to brown without the development of tints, or occasionally some yellowing developed. The method of defoliation in this series was peculiar in that whilst in other series defoliation proceeded from the bases of shoots to the tips, the tip foliage being the last retained, under this treatment defoliation generally occurred from the tips of the shoots towards the bases so that the tree retained leaves around the "crutch" last of all.   This point was clearly shown in the cases of apples and gooseberries. The condition of the barks was normal.

The yields of fruits were reduced to a certain extent.   Root systems were usually somewhat smaller than those of plants receiving the complete nutrient solution, and they generally lacked good growth of fine fiber.   Under this treatment the development of the root system appeared to be rather uncertain in the case of the apple.

OMISSION OF PHOSPHORUS

The effects of this treatment were almost as severe as those resulting from the omission of nitrogen. Times of opening of blossom and leaf buds were appreciably delayed. Blossom formation was greatly restricted owing to the death of lateral buds and the blossoms formed were weak.

The foliage exhibited very distinctive characters.   The amount was very small and was usually limited to rosettes at the tips of the shoots. Leaf size was appreciably reduced. In the early spring the leaves were practically normal in color but they soon became a dull green and developed brownish spots and later exhibited purple tints over their entire surfaces. These tints were strongly developed on gooseberry and strawberry plants whilst the spotting was most marked on the black currant bushes. After a short time the purple tints generally faded to a bronzed color, after which the leaves usually dried out in patches and were abscised. During the first season plants under this treatment generally

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[3] The above condition of the leaves is identical with one of common occurrence in fruit plantations in England usually referred to by fruit growers as "leaf scorch."

TABLE 2. SHOOT GROWTH OF APPLE TREES

Series	Season 1921 (1st season)			Seasons 1921–23*			Season 1924+		
	No. of trees	Average per tree, total shoot growth, mms.	Length of longest shoot, mms.	No. of trees	Total length shoot growth, mms.	Total weights shoots as prunings, gms.	No. of trees	Total length shoot growth, mms.	Total weights shoots as prunings, gms.
Complete Nutrient Soln:	5	939	256	5	4240	656	4	3945	58.7
Nitrogen Omitted	5	560	133	5	330	284	4	100	0
Potassium Omitted	5	608	139	4	2010	331	3	2110	21.0
Phosphorus Omitted	5	764	161	5	1330	344	3	230	0
Calcium Omitted	5	1120	226	5	4330	776	4	5275	74.1
Magnesium Omitted	5	924	177	5	3010	630	4	3225	55.1
Water Only	5	629	134	5	520	294	4	120	0

* Data for length of shoots relate to growth made during season 1923. Those for weights relate to weights of shoots made over seasons 1921–1923.
+ Data for trees on Malling No. 1. stock only.
It was not possible to take prunings from trees in the "nitrogen omitted," "phosphorus omitted," and "water only" series.

SHOOT GROWTH OF BLACK CURRANT BUSHES, SEASON 1922–1924.

Series	Season 1922 (1st season)			Season 1923					Season 1924+		
	No. of bushes	Total shoot growth, mms.	Average per bush, total shoot growth, mms.	Length of longest shoot, mms.	No. of bushes	Type of Shoot	Total shoot growth, mms.	Average per bush, total shoot growth, mms.	Length of longest shoot, mms.	No. of bushes	Total shoot growth, mms.	Average per bush, shoot growth, mms.
Complete Nutrient Soln:	10	7510	751.0	180	8	Normal	25995	3249.3	465	8	24885	3110.6
Nitrogen Omitted	10	2520	252.0	105	8	Thin	1530	191.3	125	8	1110	138.7
Potassium Omitted	10	5185	518.5	165	8	Normal	16915	2114.4	410	7	15680	2240.0
Phosphorus Omitted	10	7205	720.5	190	8	Thin	3785	423.1	160	8	4715	589.4
Calcium Omitted	10	7540	754.0	180	8	Normal	22300	2787.5	410	8	25065	3133.1
Magnesium Omitted	10	8620	862.0	215	8	Normal	21520	2690.0	475	8	24035	3004.4
Water Only	10	2550	255.0	95	8	Thin	505	63.1	50	8	980	122.5

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During the early part of each season, the leaves were normal in color but from June onwards abnormal characters developed. These characters were specific for each plant. In the case of the apple a patch of tissue dried out near the center of the leaf around the midrib, turning first of all pale green in color and quickly changing to brown following the death of the cells in the affected area. The patch generally increased somewhat in size and sometimes extended outwards between the veins towards the margins until practically the whole of the leaf was brown. This condition we have termed "blotch". It is of interest to compare its development with that of marginal "scorch" which resulted from potassium starvation, as in the former case death of the tissue commences at a central point around the midrib and extends outwards towards the leaf margin, whereas in the latter death of the tissue commences around the margin and extends inwards towards the center of the leaf.

In the case of the black currant the central portion of the leaf became purple and this developed over the surface until finally only a narrow marginal band remained green. The leaf at the same time became curled towards the under surface.

Raspberry leaves first of all developed a yellow patch in the center, a fairly broad band around the margin remaining green. A narrow yellow band then developed around the margin, leaving a narrow green band between the two yellow areas.

Strawberry leaves developed areas in the same manner as those of the raspberry but the center patches showed reddish or purplish tints.

The gooseberry differed from the other plants in that the characters developed commenced in the region of the leaf margin. Broad red bands were developed around the margins and these gradually broadened towards the center of the leaves. As this proceeded the red tint faded to yellow, the final color being a faded yellowish red.

In all cases the development of the above characters was followed closely by the abscission of the leaves. Shoot growth was usually similar to that of plants receiving the complete nutrient solution.

Defoliation was always hastened by this treatment and in the cases of apples and raspberries it often occurred very early in the season, following quickly on the development of the characteristic leaf abnormalities. Where defoliation occurred very early in the season in this way, new foliage was often developed, showing that defoliation was not due to cessation of growth activities. Compare defoliation in omission of potassium series.

The conditions of the barks were normal. The yields of fruit did not appear to be much affected and no abnormal characters of the fruits were noted. The plants developed good root systems but in practically every case examined a considerable amount of root killing appeared to have occurred.

OMISSION OF SULPHUR

Experiments on the omission of sulphur were commenced at a later date than those for the elements described above and the records for the treatment are

TABLE 3. CROPPING OF STRAWBERRY PLANTS—SEASONS 1921–23

Season	Series	No. of plants	Total No. of fruits	Total weight of fruit, gms.	Average weight of fruit per plant, gms.	Average weight per fruit, gms.
1921	Complete Nutrient	10	131	513.8	51.4	3.92
	Nitrogen Omitted	8	49	191.4	23.9	3.91
	Potassium Omitted	10	76	279.2	27.9	3.67
	Phosphorus Omitted	9	83	356.1	34.0	4.29
	Calcium Omitted	10	90	358.8	35.9	3.99
	Magnesium Omitted	10	119	483.4	48.3	4.06
	Water Only	10	51	170.6	17.1	3.34
1922	Complete Nutrient	10	91	266.8	29.6	2.93
	Nitrogen Omitted	6	10	18.4	3.1	1.84
	Potassium Omitted	9	67	193.8	21.5	2.89
	Phosphorus Omitted	7	39	85.3	12.2	2.19
	Calcium Omitted	8	42	114.4	14.3	2.72
	Magnesium Omitted	8	60	174.4	21.8	2.91
	Water Only	9	7	12.1	1.1	1.73
1923	Complete Nutrient	10	110	471.0	47.1	4.28
	Nitrogen Omitted	5	3	9.7	1.9	3.23
	Potassium Omitted	9	87	345.4	38.4	3.97
	Phosphorus Omitted	6	32	116.6	19.4	3.64
	Calcium Omitted	8	136	554.3	69.3	4.08
	Magnesium Omitted	8	92	321.3	40.2	3.49
	Water Only	8	9	24.6	3.1	2.73

TABLE 3. (CONTD.)

Season	Series	No. of plants	Total No. of fruits	Total weight of fruit, grms.	Average weight of fruit per plant, grms.	Average weight per fruit, grms.
Totals 1921–23	Complete Nutrient		332	1251.6		
	Nitrogen Omitted		62	219.5		
	Potassium Omitted		230	818.4		
	Phosphorus Omitted		154	558.0		
	Calcium Omitted		268	1027.5		
	Magnesium Omitted		271	979.1		
	Water Only		67	207.3		

TABLE 3b. CROPPING OF BLACK CURRANT BUSHES—SEASON 1925

Series	No. of bushes	Total No. of fruits	Total weight of fruits, grms.	Average weight per fruit, grms.
Complete Nutrient	10	828	497.5	0.60
Nitrogen Omitted	10	113	34.7	0.31
Potassium Omitted	10	644	257.7	0.40
Phosphorus Omitted	10	381	113.8	0.30
Calcium Omitted	10	1076	611.3	0.57
Magnesium Omitted	10	951	536.0	0.56
Water Only	10	105	33.6	0.32

not so complete as in the above cases. At the present stage of the investigation it may be said that plants under this treatment have made slightly smaller growth than those receiving the complete nutrient solution and in general have behaved like plants receiving a slightly restricted nitrogen supply. Thus the color of the foliage has been slightly pale green, defoliation has been hastened to a small extent, and during defoliation brilliant orange tints have been developed. Root systems were fairly normal. Data on blossoming and fruiting were not obtained.

RAIN WATER ONLY

The plants receiving this treatment were almost identical in every way with those receiving omission of nitrogen treatment. The tints developed by the foliage were usually rather redder than those of the latter series.

II. Experiments on the Ratio of Nutrient Elements

In these experiments attention has been given to the ratios nitrogen/potassium and potassium/magnesium in the nutrient solution.

The first experiments were made on the nitrogen/potassium ratio.

It had been found in the original deficiency experiments on apple trees that the trees receiving the complete nutrient solution showed symptoms of potassium starvation, that is, leaf scorch, though to a less extent than the trees receiving the omission of potassium treatment, whilst trees in the omission of nitrogen series showed no signs of potassium deficiency.

It thus appeared that the presence of nitrogen in the nutrient was conducive to the development of leaf scorch whilst the presence of potassium tended to check its development. A series of experiments was run accordingly in which apple trees were supplied with nutrients containing various ratios of nitrogen/potassium. It was found in these experiments that whenever high amounts of nitrogen were present in the nutrient solution it was necessary to give high amounts of potassium also, or leaf scorch resulted.

In carrying out these experiments, it was observed that where extremely high amounts of potassium were used, although leaf scorch was completely checked, the foliage did not remain healthy but showed symptoms identical with those previously associated with magnesium deficiency. In order to test whether this condition was due to magnesium deficiency, series of experiments were run using apple trees and black currant and gooseberry bushes in which plants were supplied solutions containing varying ratios of potassium/magnesium. It was found with all three test plants that when the amount of potassium in the original complete nutrient solution was trebled without altering the amount of magnesium present, the plants to which this "high potassium" solution was given showed typical symptoms of magnesium deficiency, whereas when the amount of magnesium in the original solution was also trebled no signs of magnesium deficiency were noted.

From these two series of experiments, it thus appears that, in carrying out experiments on the nutritional requirements of fruit plants, attention should

be given to the ratios of certain of the essential elements used in the nutrient solutions.

III. Experiments on Acidity and Alkalinity

Experiments on acidity and alkalinity have been carried out in sand culture on all types of plants used in the deficiency experiments.

An attempt has been made to supply the plants with the complete nutrient solution used above, with the reaction adjusted to the three values pH 3.0, 6.8, and 9.0. So far the experiments have failed to yield significant results, possibly owing to the fact that the pH values of the solutions have been altered by contact with the sand, leachings from the bottoms of the pots generally having values slightly over pH 8.0, irrespective of the original value of the solution added.

The only result which has been obtained so far has been with strawberries receiving treatment with the nutrient solution pH 3.0. In this case although the leachings from the pots showed values above pH 8.0 during the whole of the season, the plants were practically killed by the treatment. The growth made during the spring was fairly normal but during the summer the older foliage became partially dried off whilst the young foliage which was developed on young crowns dried out and withered at an early stage, and by the end of the season all the plants under the treatment were dead or almost so. The result appeared of interest because of the fact of the killing of the very young foliage which phenomenon has not been observed as the result of any deficiency treatment.

The root systems of these plants were very small and blackened.

THE INHERITANCE OF ACQUIRED CHARACTERS IN GRAFTED PLANTS[1]

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It is known that the possibility of sexual crossing of autonomous plants is quite limited under normal conditions. Nature has established two prinipal barriers to prevent crossing between species too distantly related. These are, first, the specific arrangement of the stigmatic exudation, which, in favoring, retarding, or preventing the crossings of certain pollens assures crossing between races, resulting in self fertilization, and prevents abnormal hybridizing; second, the indifference or aversion of male and female gametes, which attract or repulse each other according to their specific chemical constitutions.

It is well established to-day by experiment, and I will cite examples, that the grafted plant, once the union is realized, concentrates or dilutes the nutritive liquids in the associated parts and more or less alters the chemical constitution as a whole. The two fundamental obstacles to abnormal crosses will thus be modified in different degrees in the symbionts; the variation of the composition or concentration of the sexual fluids and gametes will be able to cause fertilization in plants normally sterile in a given situation, or even to prevent it in others which are fertile in an autonomous state.

Examples of increase, reduction, or suppression of fertility by the act of grafting are not at all rare. Thus, when *Vitis vinifera* is grafted on *V. riparia*, it produces more rapidly and more abundantly; with *V. rupestris* the opposite occurs. Plants which have lost the ability to produce seeds can sometimes recover it following grafting upon certain closely related species, as did Donaldson's Passion flower cited by Darwin.

We know, moreover, that symbiotic life in exceptional cases, as rare as they are abnormal, determines the appearance of symbiomorphoses[2], and grafted hybrids[3], the existence of which was so warmly contested some years ago, is no longer doubted.

In the presence of these variations of grafted species, it was natural to find out whether the associates alone were influenced or whether their descendants themselves were. In a word, it was necessary to determine whether they had

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 18, 1926.

[2] Daniel, L. Les Symbiomorphoses. Revue bretonne de Bot. 19xx.

[3] Daniel, L L'hybridation asexuelle Revue gén. de Bot. 1914–1915; Daniel, L. Les hybrides de greffe. Compt. Rend. du Congrès de Génétique d'Amsterdam, 21 Sept. 1923; Daniel, L. Nouvelles observations sur les hybrides de greffe et l'hérédité chez les plantes greffés. Revue bretonne de Bot. 1924.

or had not inherited the characters acquired by the grafted plants, and if the affirmative is true, to what extent this phenomenon occurs. The question is one of fundamental importance, since it concerns theories regarding "species" (fixed or variable) and at the same time the practical applications which can result from it (establishment of new varieties).

The art of grafting has been known since the most ancient times, for the sacred Chinese books, dating back more than 6000 years before Christ, mention it as a current operation. In spite of this, neither the influence of the symbiont upon the possibility or the relative facility of crossings, by changing the concentration of the fluids and the possible modifications of sexual elements (composition and chemical charge)—nor its action upon the descendants of the associated organisms whether they are rapid or rather slow, had been studied up to the end of the last century.

Occasional authors in the past centuries have suspected the possibility of the inheritance of characters acquired following grafting. Thus Dany de Brossard[4] attributes the differences between young plants arising from the seed of grafted apples to this operation. Jacques Boyceau[5] admits the influence of the symbiotic life upon the seed of the associates. At the end of the 17th century, the second Beal[6], wrote, "After many grafts, carefully observed and carried out, one may expect, if the seeds are put into good earth, those derived from the grafted plants to have some new species or a mixture".

Nevertheless, no exact experiment or technique had been devised upon this point at the time when I undertook my researches (1890). The work was thus essentially new.

We can explain the absence of documents upon these questions, when, on the contrary, the literature relative to the effect of grafting is so voluminous, by the fact that the learned men have hitherto neglected this as an art reserved for those in the profession of horticulture, and as an operation often encountering inexplicable results and sometimes apparent contradictions for those who possessed no "fil d'Ariane" capable of guiding them through the labyrinth of facts accumulated in the course of centuries.

On the other hand, as grafting is usually practiced with fruit trees, in order to judge from their progeny it is necessary to wait a long time for the fruiting of the young seedlings, so long, in fact, that the life of one man does not often suffice.

Thus I chose for the beginning of my studies herbaceous plants—annuals, biennials, perennials, the descendants of which I could very easily control for a period long enough for the individuality to become fixed.

In this type of research, as in all others which concern experimental sciences, many difficulties were met and carefully solved. The following are some of the considerations.

[4] Brossard, Dany de. La manière de semer et faire pépinieres de sauvageons, entre touts sortes d'arbres et faire vergièrs, Paris, 1638.

[5] Boyceau, Jacques. Traité du jardinage, Paris, 1638.

[6] Beal, D. Transactions philosophiques et Collections académiques, partie étrangère. 4: 14–16.

(1) It is necessary to work comparatively, that is to say, to cultivate side by side under conditions as similar as possible, grafted individuals and control plants belonging to each of the associated species; the investigator must himself make these grafts and watch the experimental plants each day in order to note all their reactions, and be very sure of what occurs. Certainty cannot be complete if the observation is made by an assistant, whatever confidence one may have in him.

(2) At the moment of aestivation of the epibionts (greffons) and of the hypobionts (sujet ou porte-greffes) it is indispensable to take the necessary precautions to prevent all sexual crossing either between the associates themselves, when that is possible, or between the plants of races or species closely related. Otherwise, this factor will vitiate the results, and one will not be able to distinguish between the effect of the sexual hybridization and that of the grafting upon the decendants of the symbionts.

(3) One should not be discouraged by failures, however many there may be, but one should repeat the unsuccessful experiments, each time varying the conditions of the environment, the processes of union, and the nature of the organisms taken as epibionts and hypobionts. It is necessary to work with wild species which have not yet varied, as well as with those which have been caused to vary through cultivation, acclimation, hybridization; which are consequently already in a state of potential variation. It is important to mention that according to the plants the appearance of specific characters may be rapidly effected or, on the contrary, may be drawn out over a long period.

(4) We must avoid the sophism into which certain scholars have themselves fallen; this consists in assuming that what one cannot reproduce experimentally does not exist. Whatever one may say, a fact is a fact, and one should not neglect it, even though it is unique and in complete disaccord with certain theories which are momentarily the fad in the science. It is necessary to state it simply, while waiting for its explanation, and to guard against hiding our ignorance by employing a new word. *A priori* negation is anti-scientific; thousands of negative experiments would not negate a positive fact, duly controlled.

(5) Moreover, it is important not to fall into the other practice which consists in generalizing from exceptional facts, and in drawing exaggerated conclusions from them.

I have been constantly inspired by these fundamental principles in the course of the 36 years of research that I have devoted to the study of grafting and other horticultural operations.

In a large number of cases, I have not obtained notable variations in the descendants of grafted plants. Is that to say that I will not succeed, with perseverance, in obtaining such results, or that others will not succeed where I failed? I have this belief even less since I now know from a long experience that the results of grafting vary in considerable measure depending upon the environments and the processes of grafting; where one experimenter has failed, another will succeed, and conversely, because however one may try, one cannot attain entirely identical associations in exactly similar environments.

The facts that I am going to describe in the present paper are then almost all very exceptional. Some appeared in the first generation, others after numerous unsuccessful attempts. Variation has often been noted in a single individual, in other cases many variatons have been secured, and most frequently the resuts have been very uneven and irregular.

In certain cases the modifications impressed upon the progeny are oriented with reference to one of the associates, that is to say, the influencing symbiont transmits a more or less important portion of its specific characters as a variety, race, or species. In other cases, the variations produced by grafting are unexpected or adventitious, that is to say, they correspond either to ancestral reversions, or to new combinations, but, whatever their particular nature may be,

Fig. 1. a. Leaf of *Alliaria* officinalis, plant grown from the seed of a specimen of *Alliaria* grafted upon *Brassica oleracea*. b. Leaf from a control (ungrafted) plant of the same age grown under the same conditions.

they are caused by the symbiont, when the controls have not furnished similar results. I will indicate here, in the chronologic order of their discovery, the principal facts of heredity that I have observed.

1. *Grafts of Alliaria officinalis upon Brassica oleracea.* In 1892, I successfully grafted *Alliaria officinalis* upon the cabbage, a variety of *Brassica oleracea*, a race characterized by the formation of a head used as food[7]. I had in mind collecting the seeds of the epibiont and those of the control at maturity; I grew them comparatively in order to study the progeny. The young plants obtained from the grafted *Alliaria officinalis* appeared more vigorous and were stouter. Their leaves were greener, more succulent, and the surface was more rugose.

[7] Daniel, L. Sur quelques applications pratiques de la greffe herbacée. Revue gén. de Bot. 1894.

The petioles were much longer, the blades were of a much greater size. (Fig. 1). Evidently these changes related to characters of little specific import; they showed, however, that the symbiosis influenced the posterity of the epibiont. They thus had a chance to follow new lines in a new way.

2. *Grafts of flower buds of Brassica oleracea.* This time I chose young floral shoots of turnip cabbage as epibiont, a race in which the spherical tuberous part is found beneath the soil; I placed them on young Saint Brieuc cabbage, at the time when the stalk of the latter was the thickness of an ordinary pencil. These two grafted races differ not only in their well known morphological characters, but also in their unequal resistance to cold; in fact, the turnip cabbage freezes easily, while headed cabbage can stand the lowest temperatures of our Breton Climate.

Operating in this way, the grafting succeeds very well. The infloresences develop vigorously; they furnish flowers and seeds in as great abundance as if they were still on the parent stem. So in the following year the seeds will produce young cabbages which make plants comparable with individuals of the same age produced by the control plant.

The descendants of epibionts offer considerable variety. Their stems were tuberous in varying degrees and elongated like those of Moellier Cabbage; the leaves, produced quite close together, were more developed than those of the controls, but they remained separate and did not form a head as in headed cabbage[8].

The winter of 1893-94 was particularly rigorous; the temperature fell to $-13°$C. All the original cabbages were frozen, but the new cabbages which I had obtained resisted, thanks to the crowded leaves which, in holding themselves about the stem, formed a sort of protective cloak around the buds and tuberous swellings. In the following spring the numerous buds developed into leafy stems and produced an abundant forage.

Thus the descendants of the turnip cabbage had inherited the resistance to cold of the headed cabbage on which the parent scion had been grafted. Their origin and their qualities of resistance were verified by a commission named by the agricultural association of Chateau Gontier, the city in which the experiment had been made. The facts were confirmed in an official report.

These same cabbages were later cultivated at Rennes, for comparison alongside of other local races. An analytical study of them was made by M. Lechartier, member of the science faculty; it showed that the new race held, as regards productivity and nutritive value, a very honorable position among the other races of forage cabbage[9].

3. *Improvement of the wild carrot by grafting on the cultivated cabbage.* Following the researches mentioned, I grafted at the beginning of their second year of growth wild *Daucus Carota* on the garden carrot with the usual orange red

[8] Daniel, L. Influence du sujet sur la posterité du greffon. Le Monde des Plantes. Le Mans, 1895.

[9] Lechartier. Sur la composition comparée d'une variété nouvelle de chou Moellier et de divers choux fourragers. Bull. de la Soc. scient. et med. de l'Ouest. 1897.

root; these two types differ externally in the form of the rosette of leaves expanded in the wild plant, erect in the cultivated.

Despite the considerable differences in the size of the roots, the graft succeeded very well. The wild carrot completely absorbed the abundant reserves of the garden carrot; thus abundantly supplied, it furnished vigorous stems bearing leaves that were greener and more highly developed than usual. The inflorescences, more numerous and bearing more flowers than normally, gave rise to large achenes furnished with long spines, and thus they were clearly distinguished from those of the controls. Sown at the proper time, these achenes produced plants varying greatly in appearance[10].

Some resembled the wild type in the white, only slightly swollen root, and in the rosette of leaves spread out on the ground. Others possessed a more or less thick central root, white or yellowish, and very rarely provided with a green crown. In the form of the root and in its thickness they resembled the cultivated carrot, but they have a rosette of expanded leaves like the wild type. Some individuals displayed roots ramifying on one side, and the secondary roots were inflated like the tap-root itself.

All these varieties were entirely resistant to cold, like the wild type, although during winter they remained without care in the ground. I have followed for some years the progeny of certain of these plants which I have selected; I have shown that their characters are for the most part constant and that is is possible to fix races. But as these latter did not present qualities of any immediate practical interest, I have not kept them.

4. *Grafts of kidney beans.* The different races of *Phaseolus vulgaris*, and closely related species, may be grafted among themselves easily by employing my procedure of grafting on germination.

Having made grafts between the dwarf kidney bean Novi de Belgique and the branching kidney beans of Soissons, I sowed the seeds and studied the progeny for a long time. In most cases I have established for these plants, as for the majority of hybrids and selected races which are in a state of potential variation, some mosaique changes, some cryptomeric throwbacks, and the appearance of new characters[11].

I obtained a variety of the original black kidney beans of Belgium, which is fixed. It is the first original race of kidney beans designated as such in the genus *Phaseolus*. Since that time others have been obtained and are now in commercial use. Likewise, I have obtained a race of branching Soisson kidney beans, perennial by tuberous starchy roots.

These unexpected results show that symbiosis produces sometimes a very considerable echo in the growth rhythm of races of *Phaseolus*.

[10] Daniel, L. Amélioration de la carotte cultivée par sa greffe, sur la carotte sauvage. Compt. Rend. de l'Acad. des Sci. Paris, 1898; Daniel, L. La variation dans la greffe et l'hérédité des caractrèes acquis. Ann. Sci. nat. Bot. 1898.

[11] Daniel, L. Variations dans les caractères des races de haricots sous l'influence du greffage. Compt. Rend. de l'Acad. des Sci. 1900.

5. *Grafting Sinapis on Brassica.* These grafts succeed most easily if one uses young seedlings, especially in the spring, when the stems are about the thickness of an ordinary pencil. In general, *Sinapis alba* develops with vigor on cabbage. It produces numerous seed but they are not identical with those of the controls, from which they differ in size and color[12].

Sown in the spring for comparison with control plants and with the cabbage used in the experiment, the seeds of the epibiont gave me some germinations in which the cotyledons and hypocotyledonary axis showed a very clear analogy as to form and color with the corresponding organs of cabbage germinations. This transmission of characters did not persist long. Soon the yound *Sinapis* produced by the epibiont reassumed the characters of the species; the influence of the hypobiont upon the progeny of the epibiont was thus temporary.

6. *Grafts of bittersweet on belladonna.* Having grafted *Solanum Dulcamara* (Bittersweet) on the root of *Atropa Belladonna* (belladonna) I obtained a very significant result. The stems of the bittersweet became very hard in the neighborhood of the callous caused by the union; the principal stem rapidly ceased growing and numerous lateral ramifications replaced it in most of the individuals. Soon the branches were lying on the soil producing adventitious roots which would have compromised the graft if they had not been carefully suppressed.

The epibiont fruited; the fruits were of variable sizes, for I had pruned a part of the branches which were beginning to straggle. Four seeds were sown naturally; one of them produced a normal plant with an erect stem; two others, plants with recumbent stems like the epibiont; the fourth, a plant intermediate as regards geotropic habit between the two preceding types.

The creeping character, impressed on the epibiont is thus transmitted in a very irregular manner to its descendants. Transmission, complete for two of the descendants, has been partial in another and absent for the fourth.

This result makes possible the comprehension of the appearance of many forms that one observes sometimes in plants arising from the sowing of the seeds of grafted trees.

7. *Grafts of potatoes on tomatoes.* One of the most curious results of the grafting of the potato (*Solanum tuberosum*)on tomato (*Solanum Lycopersicum*) is the formation of aerial tubers in the epibiont. These tubers vary with regard to number, size, and color according to the grafted varieties[13].

Having grafted the Fluke on the tomato, I obtained beautiful aerial tubers of a green color that I kept through the winter and planted in the month of March of the following year. They furnished me with beautiful stems similar to the primitive variety with the exception of three individuals on which I found at the same time some subterranean tubers and some aerial tubercles. The following year aerial and subterranean tubers were carefully propagated, and all furnished normal stems. The agametic heredity of the aerial tuberization has thus been temporary and fugacious.

[12] Daniel, L. Hérédité transitoire a la suite de la greffe de moutarde sur le chou. Revue bretonne de Bot. 1919.
[13] Daniel, L. Nouvelles recherches sur les greffes herbacées. Revue bretonne de Bot 1910–1913.

In this case it is a question of vegetative multiplication; it would be very interesting to see if there might be inheritance of the aerial tuberization character through the seeds. For that, it would be necessary to obtain the fruit of the epibiont, but many varieties of potatoes do not produce fruits, or fruit very rarely. I have noticed a more abundant flowering in the Fluke when grafted on the tomato, but so far I have not obtained fertile seeds of this variety. The experiment continues and I do not despair of obtaining them at some time. Perhaps the character of aerial tuberization may be fixed by sowing the seeds of the epibiont which may have recovered coexistent with subterranean tuberization.

8. *Grafting Artemisia and Tanacetum on Chrysanthemum.* One can easily arrange grafts between the different species of composites belonging to different tribes[14]. I most often use *Chrysanthemum frutescens* as the hypobiont, a perennial frutescent species which is generally used in the decoration of our gardens, but one which freezes in the open air in our climate in winter.

When one grafts onto cuttings of this species in spring young annual stems of *Artemesia* and *Tanacetum*, these stems, instead of dying the following winter, become for the most part persistent, and the hypobiont, protected by the foliage of the epibiont—forming a protective dome—can sometimes remain in the open ground through cold spells without perishing.

Artemisia Absinthium, Tanacetum Balsamita, T. vulgare, and *T. boreale* grafted on *Chrysanthemum frutescens* lived through three or four years. But the epibiont was progressively modified. Its size diminished as well as its vigor; the internodes became shorter; the leaves smaller and twisted[15]. To these morphological modifications there correspond changes in the physical and chemical nature of the characteristic essences of these species[16]. Having collected the seeds of an epibiont of absinthe transformed in this way, in the fourth year from the graft, I sowed them at the normal time. Some germinated and I noted a stem more modified than the others. Having kept it, I sowed seeds from it the following year and obtained numerous individuals, all different from each other. There were two extreme types connected by all sorts of intermediates: one recalled the control species from its large leaves with large, expanded lobes, but the odor was disagreeable, weakened and fugacious; the other displayed leaves that were more hairy, thinner and curled, of much smaller size, with an odor more agreeable, more pronounced, and more persistent than that of the progeny of the controls. To summarize, the first type was clearly deteriorated on the whole: the second on the contrary was greatly improved. (Fig. 2).

Consequently, we see the importance of these results for medicine and for industry. The variation procured by grafting can be maintained, since absinthe multiplies by cuttings and is perennial.

[14] Daniel, L. Observations sur la greffe de quelques Composées. Bull. de l'Assoc. francaise pour l'Avancem. Sci. 1903; Daniel, L. La question phylloxérique, le greffage et la crise viticole. Paris-Bordeaux, 1906–1920.

[15] Daniel, L. La question phylloxérique. l. c.

[16] Daniel, L. L'hérédité chez les plantes greffées. Compt. Rend. de l'Acad. des Sci. 17 Nov. 1924.

With *Tanacetum vulgare* and *T. boreale*, I obtained some striking and even more complete demonstrations of variability. Seed collected from a stalk of *T. vulgare* that was grafted on *Chrysanthemum frutescens* and grown for three years from the graft (Fig. 3) were sown and produced individuals which bore leaves different from those of the control (Fig. 4). The elongate, lanceolate form was replaced by a shorter, more thick-set form, almost round; the divisions of the leaf were twisted, and the appearance more bushy. These characters

Fig. 2. Leaves from different individuals of *Artemisia Absinthium* grown from seeds of a plant grafted upon *Chrysanthemum frutescens*. These were all gradations in size between the largest and the smallest.

were more particularly pronounced in one of the individuals; some others resembled the control, and there were all gradations between these two extreme types. The odor was not the same and varied with the individuals, so that one could easily recognize them by their scent.

In the epibiont, *Tanacetum boreale*, the growth rhythm sometimes changes and the plant sends up new growth, that is to say, flowers many times in the course of the year. I collected the seeds from an epibiont which was producing

new growth and sowed them the following year. As these seeds were poorly formed only six germinated. Of the six new plants two flowered without making new growth; the four others, on the contrary, produced new growth, thus retaining the character acquired by their parent. I have kept these individuals and will thus be able to see if the character acquired is definitely hereditary.

Fig. 3. Grafts of *Tanacetum vulgare* upon *Chrysanthemum frutescens*: a, graft in the third year of development; b, graft in the first year.

On one of these stalks. I found leaves, the divisions of which instead of being opposite upon the common petiole, were alternate. This abnormal arrangement showed that the grafting had caused a disturbance of the species and presaged future variations (Fig. 4).

9. *Grafts of Helianthus annuus on H. tuberosus.* These two species of *Helianthus* have very different growth rhythms. *H. annuus* is an annual plant which produces an abundance of seed and dies at the end of summer or the beginning of autumn. It does not contain inulin in its tissues excepting after a certain system of wounding[17]. *H. tuberosus* is perennial and multiplies exclusively by its rhizomes, since in our Breton climate it produces no seeds. After the completion of growth the colorless tissues are filled with inulin.

These two species may be grafted very easily upon each other. When *H. annuus* plays the role of epibiont, it behaves in a very irregular fashion, depending upon the individuals, the moment of grafting, and the environmental conditions. Sometimes it remains simple, sometimes it branches from the base.

Fig. 4. Leaves of *Tanacetum*, seed from grafted plants: a, normal leaf of *T. vulgare*; b, leaf from a stem produced from seed of the same species; c, leaf of *T. boreale*, from an individual grafted upon *Chrysanthemum frutescens*.

The heads vary in number and size; they become almost gigantic upon the simple and stocky stems, the leaves of which are large and thick. Sometimes monstrosities appear in the leaves, or fasciations in the heads or stems[18].

In the ramifying stems, numerous heads are sometimes formed, recalling the arrangement in *H. tuberosus*. The largest are situated at the extremities of the principal axis and branches, yielding mature fruits; others are slower and less developed, not always maturing.

It may happen that the epibionts show a noticeable increase in the length of life; certain of these remain green, especially at the base, whereas the stems of the controls may have been completely dried up for a long time. Very exceptionally it happens that new flowers appear and that certain stems thus produce new growths.

[17] Schröder. Zur experimentellen Anatomie von Helianthus annuus L., Göttingen, 1912.
[18] Daniel, L. Hyperbioses de soliel et de Topinambour. Revue bretonne de Bot. 1923.

I have many times collected seeds from the largest heads of stout and simple individuals with gigantic leaves, and I sowed these seed in the spring of the following year. Young plants exhibited partial inheritance of the new characters varying according to the character considered and according to the individual plants. Thus the inheritance of dwarfing of the entire plants and of gigantism of the heads have been more marked than the others. The monstrosities have not been freely inherited; as to the character of new growth, it appears slightly in the first generation and is lost in the second.

It would have been possible by a careful and methodical selection to fix some of these variations and to obtain a thick-stemmed dwarf type, with gigantic leaves and a single head of great size[19]. As I did not have at my disposition a sufficient understanding of the basis upon which to make this selection and as I then had other more important experiments, I did not pursue the researches on the plant.

10. *Grafts of Helianthus tuberosus on H. annuus.* These grafts are the inverse of the preceeding ones and I have repeated them each year since 1894. The variety of *H. tuberosus* which I have used exclusively as an epibiont possesses white tuberous roots, is rugose, and has soft tissue reenforced with well developed ligneous strands. The surface sinuosities and cavities contain earth which it is difficult to remove by washing. This is a great fault from the point of view of food. Right here there is a very important point; this variety has never varied in my cultures, however many controls there have been; and it has never produced seeds. When this variety was grafted on *H. annuus* I noted various changes occuring at the same time by the hypobiont and the epibiont.

H. annuus over-developed its root system; its stem became two or three times thicker, its very abundant wood hardened, and its tissue was much reduced. Its life was prolonged for many months, because in the mild winter the individuals just grafted succeeded in lasting till February, while at the beginning of October all the controls were completly dried up. Up to the present I have never found inulin in hypobionts; this substance cannot then pass into them in any form, which conforms to the observation that I first made in 1891[20].

The epibiont *H. tuberosus* succeeded very well upon *H. annuus.* It furnished a vigorous stem which branched freely for the most part; its flowers were quite frequently larger than those of the control and lived longer.

Towards the completion of growth it produces abundant reserve. As it cannot form its rhizomes in the soil, since the swellings develop too high, it accumulates its sugars and its inulin in the buds situated in the axils of the leaves, and these are transformed into aerial tubers.

This formation of aerial tubers, to my knowledge, at least, has never been noted in autonomous *H. tuberosus.* It is thus a question of a character which appears exclusively under the influence of grafting and which consequently is absolutely new.

[19] Daniel, L. Nouvelles observations sur les hybrides de greffe et l'hérédité chez les plantes greffées. Revue bretonne de Bot. 1925.

[20] Daniel, L. Sur la greffe du parties souterraines des plantes. Compt. Rend. de l'Acad. des Sci. 21 Septembre, 1891.

Sometimes the aerial tubers are basally located, that is to say, situated in the lower part of the stem of the epibiont; they are then rugose, of a dark violet color, and usually leafless. Sometimes they are apical, that is to say, situated near the summit of the stems, which no longer have heads or bear only a small number of them; they are, in this case, elongate and almost cylindric, more rarely mammiform; their color is dark violet.

In some epibionts, rather rarely, the leaves assume a purplish brown tint, more pronounced on the upper surface, but also found on the nerves of the under surface.

When the year is humid or when the epibionts are protected from the direct rays of the sun, one sees the formation at the base of the stems of adventitious roots, as numerous as those which arise at the usual base. If they could reach the ground, they would cause the breaking up of the union and the rupture of the association. Since they are always located at a distance from the ground, they dry out at their tips and remain in the condition of stumps. It is thus a new character produced by the symbiosis. Sometimes the base of the epibiont enlarges abnormally and produces an almost cylindrical, irregular crown of excrescences which contains reserve food. These parts are frequently attacked by snails and wasps which are fond of the sweet liquids which ooze out of the wounds.

Following the observations of Maule and Carriere, I have myself seen rarely on the stem of *Helianthus annuus*, as hypobiont, deep in the soil, small subterranean fusiform tubers, like the roots of Dahlia (see foot note [18]). These roots do not belong to the hypobiont; they resulted from an intercalary growth of roots produced and thrust downward by the epibiont, *H. tuberosus*, which are, as it were, cemented to the stem of the hypobiont, *H. annuus*, up to the point where they can reach the soil. This character is due to the struggle which exists between the two associates in view of the return to an autonomous life, and the conservation of the individual; it never appears in the autonomous *H. tuberosus*.

Another important fact likewise due to grafting, is the augmentation of the aerial parts of the epibionts. Save for the subterranean tubers destined to propagate the species, the controls were entirely dried up by the end of November but the epibionts remained green and living longer, that is, the entire plant. They finally die progressively from the upper extremities, but even at the end of January, February, or sometimes in March, one still finds green parts in the neighborhood of the scarred tissue.

The aerial tubers continue living quite a long time; if they fall on the ground through the breaking of the stem which bears them, they rapidly take root and produce a new stem. If it is a question of basal or apical tubers the plants derived from them have so far produced no aerial tubers. This character then is not continued by agametic (vegetative) reproduction under the conditions of the experiment.

It was interesting to see what would happen to the descendants of the grafted *H. tuberosus*, if one could in some way make them produce seeds. For seventeen years, I vainly attempted to bring about this result, when at last in 1921, I

Fig. 5. Leaves from young plants produced from sowing seed of a specimen of *Helianthus tuberosus* grafted upon *H. annuus*.
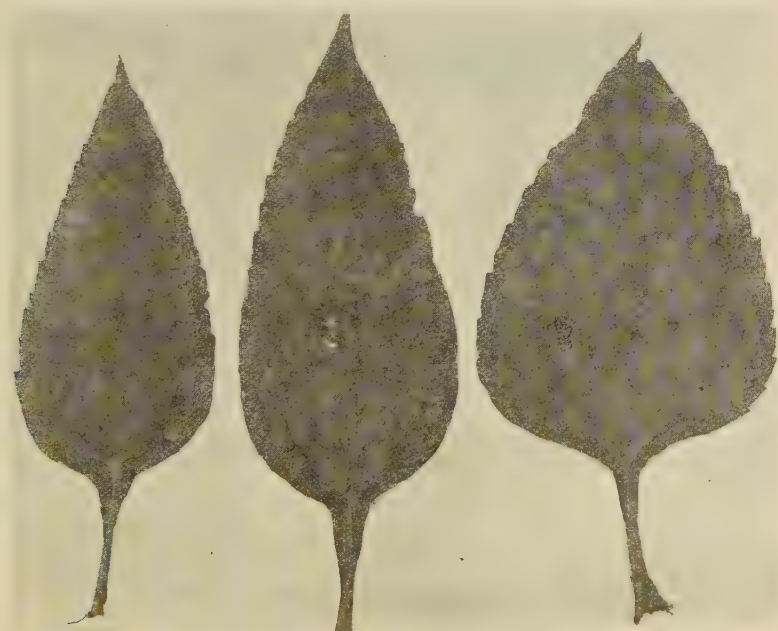
Fig. 6. Leaves from three other plants produced by sowing seed of a specimen of *Helianthus tuberosus* grafted upon *H. annuus*.

had the good fortune to collect 36 of these seeds, apparently well formed from an epibiont growing in the full sunlight isolated against the side of a wall; the latter bore at the same time seeds and aerial tubers.

In the following spring, I planted the aerial tubers and I sowed the seeds. The former, as usual, produced some normal plants; the later did not germinate

Fig. 7. a. From a sowing of *Helianthus tuberosus* with aerial tubers and numerous subterranean tubers (transitory heredity). b. From a sowing of *H. tuberosus* with aerial tubers and a small number of subterranean tubers (*H. tuberosus Dangeardi*, with persistent heredity).

at all. Fourteen of the former developed new plants which differed from the original variety in the form and venation of the leaves (Figs. 5,6.), in the size of the vegetative growth, the color of the green parts, the relative precocity of the inflorescence, the size and number of the heads, etc.

In October, I examined the subterranean tubers without troubling about the aerial tuberization which had not yet begun. I noticed remarkable differences in form, number, size, color, and arrangement. Some were elongate, smooth, and distant from the crown; others were ovoidal or spherical, rugose, and grouped around the crown as in the parent variety. Certain plants bore 6 or 8 kilograms of tubers while others were reduced to a hundred grams.

I chose six of the most diverse varieties and planted them anew in October 1922, four tubers from each. In the course of the summer of 1923, I established

Fig. 8. Stem of *Helianthus tuberosus Dangeardi* with aerial tubers, in perfect state of vegetation. Photographed Mar. 15, 1926.

the fact that all retained their particular characters. This time I collected only the subterranean tubers in mid-November and I saw with astonishment that certain new types bore subterranean and aerial tubers[21].

One type had aerial tubers only on one of the stalks (Fig. 7a); its subterranean tuberization was considerable. The inheritance of the aerial tuberization character had been partial, since all the individuals did not possess it. The in-

[21] Daniel, L. Hérédité d'un caractère acquis par greffe chez le Topinambour. Compt. Rend. de l'Acad des Sci. 1923.

heritance was fugacious in the individual where it was first manifested, for it had not reappeared in 1924.

Another type with reduced subterranean tuberization (Fig. 7b) bore aerial tubers in variable numbers on the four individuals that I have multiplied. I planted comparatively in March, 1924, the subterranean and aerial tubers of this variety; the aerial tuberization reappeared.

In 1925 I made the experiment on a much larger scale; this time I planted 335 aerial and subterranean tubers of the variety that I had referred to under
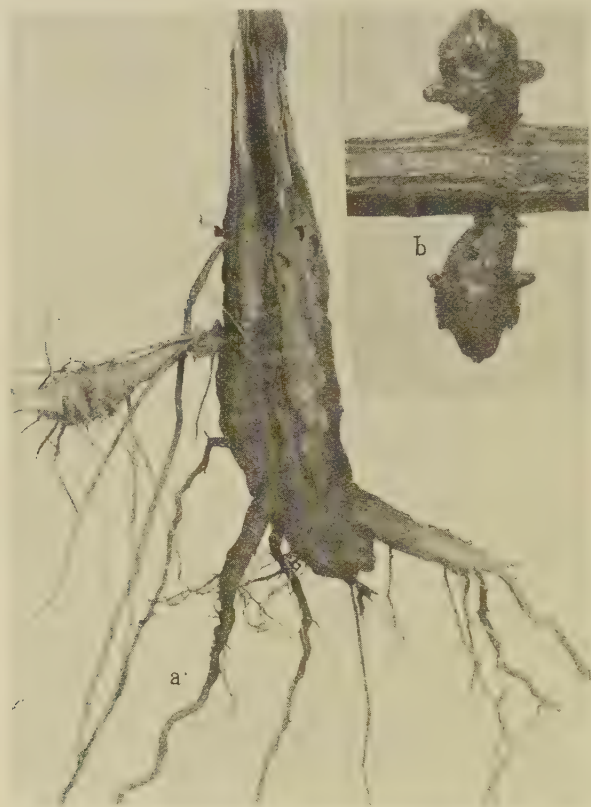
Fig. 9. *Helianthus tuberosus Dangeardi.* a. Base of stem swollen, with a subterranean tuber and some tuberous roots. b. Stem with two opposite aerial tubers.

the name *H. tuberosus Dangeardi*. I have noted that the aerial tuberization of the individuals has been more or less emphasized, more or less precocious both according to the individuals and to the time of planting. But some aerial tubers were apparent in all; so the inheritance of this acquired character has been very clear after four consecutive years of vegetative multiplication.

Moreover, I have observed very clearly the inheritance of other characters, caused by the struggle existing between the symbionts whose modes of development and reproduction are so different.

With *Helianthus tuberosus Dangeardi* we find:

1. Adventitious roots in the form of stumps piercing the bark of the erect stems, with growth arrested early in the open air, but rooting easily if blown down on the ground by the wind. The latter then forms a thick mat, in the basal section (Fig. 8).

2. A basal, tubercular ring, comprising irregular excrescences in the parenchyma of which abundant reserves have accumulated (Fig.1 9).

Fig. 10.   a. Stem of *Helianthus tuberosus Dangeardi* producing at the left a strong root tuberously enlarged. b. Aerial tuber which has endured during the winter −8°C. Photographed Mar. 15, 1926.

3. Some tuberous roots recalling those of dahlia (Fig. 10) or swollen like beads (Fig. 11). These roots were composed of a small woody cylinder surrounded by a thick layer of reserve woody parenchyma. This is the first example of the appearance of tuberous roots in *H. tuberosus*, the reserves of which in the autonomous state are exclusively disposed in the rhizomes.

Moreover, the majority of individuals succeeded in living much longer than the controls, for the basal parts were still green at the end of March, 1926, while the corresponding parts of the controls were completely dried up in mid-November, 1925. Thus they had resisted low temperatures of $-8°C.$ as had also a large number of aerial tubers (Figs. 9, 10). I presented specimens of these

Fig. 11.   Stem of *Helianthus tuberosus Dangeardi*, with one root producing tuberous swellings in a chain and matted with roots over the point touching the soil. Photographed Mar. 15, 1926.

plants (Figs. 9, 10, 11, 12) at the meeting of the Academie des Sciences de Paris, March 13, 1926.

Some individuals have retained the greenish yellow color of the leaves and stems of the control variety, others possess a very intense brownish red color, particularly bright on the veins of the leaves. The latter, besides, have lasted much longer than the leaves of the control.

Conclusions

The results that I have just briefly presented are based on facts which have been verified by competent persons. I possess the specimens of the perennial varieties that I have obtained. I have distributed some cuttings or tubers of these and I still have some of them for distribution to scientists who would like to study them. In this way their authenticity cannot be doubted.

Fig. 12. Two specimens of *Helianthus tuberosus Dangeardi*.
a. Stem erect, with aerial tubers bearing no roots. b. Stem procumbent, with an aerial tuber bearing roots and numerous mats of aerial roots. Photographed Mar., 15, 1926.

They permit the formulation of interesting practical and theoretical conclusions.

Theoretically, they deomonstate for the first time experimentally the accuracy of Lamarck's hypothesis relative to the inheritance of acquired characters due to variations of the environment.

In fact, in the graft of *Helianthus tuberosus* on *H. annuus* the antagonism between the periodicity of growth and of reproduction of these two species has pro-

voked special reactions, and the appearance of essentially new characters in the epibiont. Never, in reality, has one observed in the autonomous *H. tuberosus* aerial tubers or tuberous roots, the mat of aerial roots, the persistence of life in the aerial stems, and a resistance to temperatures of $-8°C$.

The *novelty of characters* is precisely one of the requirements laid down by the adversaries of the theory of the inheritance of acquired characters.

Moreover, these new characters, due exclusively to the graft factor, have been *acquired since the first sexual generation* and have been *retained for four successive years*; this is the second condition demanded by these same opponents before admitting as convincing an example of the inheritance of acquired characters. So, from this time on, we may say that the latter has been experimentally proved.

Practically, the results demonstrate that grafting is not always, as has been said, the perfect method of retaining variations, but that it is, in certain cases, a powerful agent for transformation, capable of causing the formation of new varieties and, with this indication it interests those who hope to obtain new forms. As to the fact that the variations produced by grafting are exceptions, they are therefore only the more valuable, for these are precisely the rarities which are sought after in horticulture.

The modifications caused by grafting, whether in the symbionts themselves, or in their descendants, may be useful or not, and some may even continue deteriorations of the grafted type. As a rule only the improvements will be multiplied; the other variations should be retained only as material for study.

POLLINATION AND LIFE HISTORY STUDIES OF LETTUCE (LACTUCA SATIVA L.)[1]

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INTRODUCTION

The lettuce crop is a very important one in California. In 1918 California shipped 2051 carloads of lettuce and in 1925, 21,623 carloads. In 1923, 1924, and 1925, approximately 40, 60, and 60 per cent of the carlot shipments of lettuce in the United States originated in California. The lettuce seed growing industry is also one of considerable importance. The variety New York is grown exclusively for shipping. For the production of seed, however, all of the standard varieties are grown. The growing of lettuce seed is restricted almost entirely to the delta lands of the Sacramento and San Joaquin rivers and to the Santa Clara Valley. Whenever a large number of varieties are grown in close proximity there arises constantly the question of possible cross pollination. The main object of the pollination studies was to answer this question. The morphological studies made to furnish information needed in order to prosecute more successfully other lines of investigation that have been started on lettuce and to ascertain the facts regarding floral development, spermatogenesis, oogenesis, fertilization, and development of the embryo, seed, and fruit.

The lettuce variety used was Iceberg. The observations were made and samples collected on material grown at Davis, California.

Development of the Flower. In order for the main flowering stem or central axis to develop normally it is usually necessary in the case of most heading varieties to quarter the heads or else remove the upper leaves entirely. This operation is usually performed before the head becomes hard and while the stems are short. If quartering is delayed until the stem has elongated there is danger of injuring it.

The oldest flower head terminates the main axis. When the axis is about eight inches long differentiation of the floral organs is first noted. The meristematic region of the receptacle, at first convex, becomes flattened and broadened; and following this there arise simultaneously over the entire surface, the protuberances that give rise to the individual florets. The outline of these papilla-like projections soon becomes angular, and the appearance of a marginal ring of cells is the beginning of the corolla tube. Swellings, which soon appear upon the inside of the corolla tube, are the stamen primordia. An elevated meristematic ring of tissue near the base of the corolla tube and on its outer side gives rise to the pappus. The stamens and pappus appear almost simulta-

neously. The carpels are the last organs of the flower to differentiate. By the time the carpels appear, the corolla has started to curl inward. The cavity of the ovary is soon formed as a result of the upward growth of the carpellary tissue.

Oogenesis. The ovule arises at the base of the ovarian cavity. At the time the hypodermal archesporial cell is differentiated the anthers are in the pollen mother cell stage. The archesporial cell (megaspore mother cell) stains deeply and is enclosed within a single layered nucellar tissue. The unilateral growth of the single massive integument causes the ovule to assume finally a position of complete anatropy. The nucellus never consists of more than a single layer of cells. The ovule is completely inverted by the time the heterotypic divisions are initiated.

By two successive divisions the four megaspores are formed with the haploid number of chromosomes. A wall forms between the two daughter cells after the completion of the heterotypic division. Walls are again formed at the completion of the homotypic divisions, giving a linear series of four megaspores of equal size. The three micropylar megaspores soon degenerate as a result of encroachment upon them by the functioning, innermost megaspore. The nuclear cells abutting on the micropyle appear to enlarge slightly for a time. The rapidly growing embryo sac, however, soon crowds the lower cells of the nucellus and the degenerating megaspores into the upper end of the micropyle to form the so-called nucellar cap.

The first nuclear division of the functioning megaspore occurs near the middle of the embryo sac. The daughter nuclei then migrate toward opposite ends and by two successive divisions each forms four free nuclei at the extremeties of the sac. The polar nuclei move toward the center and finally come to rest just above the egg.

The mature egg projects above the synergids into the embryo sac for some distance. Its nucleus is imbedded in a deeply staining mass of cytoplasm at the summit of the egg.

The polar nuclei are quite distant from one another two hours before anthesis, and, so far as has been determined, fusion of the polar nuclei does not take place until the time of fertilization.

Not more than three antipodal cells were ever observed. These have no definite arrangement. Sometimes they are in a linear row completely filling the antipodal neck of the embryo sac. In other cases, the two lower antipodals lie side by side with the third cell forming a triangle.

Spermatogenesis. The archesporial cells of the stamen are differentiated early, the first periclinal walls cut off a single linear row of pollen mother cells on the inside, and an outer layer, which divides to form the tapetum, the middle layer, and the endothecium. The pollen mother cells and their nuclei enlarge considerably before the heterotypic divisions are initiated.

The spindles of the homotypic division extend in opposite planes. According to Gates and Rees ('21) "after the reduction divisions the cytoplasm of the pollen mother cells begins to constrict at four points and these constrictions finally meet at the center, cutting the contents of the cell into four parts." Pollen grains of samples collected several hours before anthesis have two filamentous sperms and

a vegetative nucleus. The sperms at this time reach about half way around the interior wall of the pollen grain.

Pollination. About twenty-four hours preceding anthesis, the bracts subtending the flower head start to open at the summit due to the development of the individual flower buds. The flowers open in early morning. The time of opening is probably largely dependent upon the temperature. The higher the temperature the earlier the flowers open. They close usually within an hour or two and do not open again. At time of anthesis when the floral organs are fully extended and expanded the brush hairs of the pistil are covered with pollen and the stigmatic lobes have made almost a complete spiral backwards. Among lettuce and seed growers it is the belief that this plant is entirely self-pollinated.

The lettuce flower is probably almost entirely self-pollinated. The mechanism, however, is such that crossing can take place. When the pistil elongates and pushes its way through the anther tube, the brush hairs on the side of the pistil sweep the pollen grains upward out of the pollen sacs of the dehisced anthers. Oliver ('10) is of the opinion that self pollination is brought about by pollen falling on the inner face of the stigmatic lobes when the latter expand. Knuth ('98) on the other hand, states that when the stigmatic lobes expand, they make a complete revolution backwards and the stigmatic papillae come into contact with the pollen held by the brush hairs of the pistil, thus bringing about self pollination. Observations were made in methods of natural pollination in the White Paris Cos variety of lettuce in June, 1916, at Davis, California. A number of flower heads were protected against insect visitation. When the stigmatic lobes were fully expanded the number of pollen grains that had fallen on the inner surface of stigmatic lobes of each flower was counted. Seventy flowers were observed, of these 58 did not have any pollen grains on the inner stigmatic surfaces. The number of pollen grains on the inner stigmatic surfaces of the other 12 flowers ranged from 1 to 7. It was also found that only occasionally do the stigmatic lobes make a complete revolution backwards either on the flowers that are protected from insect visitation or that are visited by insects. Flowers were observed at the time when they were fully expanded and also after they were closed.

The number of pollen grains on the surface of the stigmatic lobes of flowers that were insect visited were also counted. Seventy flowers were observed. The number of pollen grains on the inner stigmatic lobes of each flower ranged from 4 to 51. One plant observed had 169 flower heads open on June 26. During the short time these flowers were open 88 of the flower heads were visited by insects and some of those flower heads were visited a number of times. On the same day another plant had 82 flower heads open and 60 of these were visited by insects. There is nothing to prevent foreign pollen being brought in by insects. It is not known whether pollen other than that on the inner surface of the stigmatic lobes and not in contact with the stigmatic papillae can penetrate the pistil and function in fertilization.

Anthesis. In 1925, studies were made of a number of lettuce plants of the Iceberg variety in order to determine the waves of anthesis occuring throughout the season and the length of time required for the seeds to ripen. The plants observed had flowers in bloom for the first time on June 11. The flower heads

were counted each morning at the time of anthesis. Almost all the plants reach-
ed a flowering peak in the latter part of June, after which period occurred a drop
to zero in some cases for several days and then another peak of less magnitude
in July. The morning following a very warm day there is usually a decided rise
in the flowering curve; the morning after a cool day there is usually a pronounced
drop. The influence of temperature is more noticeable during the early than dur-
ing the latter part of the flowering period. Although different plants may start
flowering at the same time, their flowering curves seldom parallel one another.

Ripening of the Achenes. Within two or three days after anthesis the withered
corollas, dehisced stamens, and shriveled styles and stigmas are shed in a cluster.
The bracts then close tightly about the developing achenes. The beak of the
young fruit elongates very rapidly and carries the pappus along in its upward
growth. When the seed is ripe the pappus expands. Each day all the seed heads
that ripened their achenes were counted and then removed. During the time of
these studies in late June and July the average time from anthesis to fruit ma-
turity was about twelve days.

Fertilization. In June 1924 a study was made to determine the length of time
between pollination and fertilization and also the method of embryo and en-
dosperm development. The study was started the morning of June 12. The Ice-
berg variety was used. The table gives a record of the temperatures taken in the
shade of the lettuce plants in the field.

TABLE 1. TEMPERATURES IN THE SHADE, JUNE 12, 1924

Time	Temperature Degrees C.	Time	Temperature Degrees C.
5 A.M.	12.0	1 P.M.	31.0
6 A.M.	13.5	2 P.M.	31.8
7 A.M.	16.0	3 P.M.	31.4
8 A.M.	21.5	4 P.M.	28.8
9 A.M.	24.0	5 P.M.	27.0
10 A.M.	26.5	6 P.M.	25.0
11 A.M.	28.6	8 P.M.	18.0
Noon	29.4	10 P.M.	14.5

At 8 A.M. the flowers were expanded and the pistils fully extended. Eight
o' clock is hereafter referred to as the time of pollination, representing the mean
rather then the exact time of pollination.

At 11o'clock of the same morning sperms were first observed in the embryo
sacs. There were only a few embryo sacs that contained sperms at this time.
At noon a few more of the embryo sacs had sperms in them. By 1 P.M., or
five hours after pollination, the majority of the embryo sacs contained sperms.
In samples taken at 2 P.M., no fertilization stages were found, but the embryo
sacs contained all stages of development from fertilized eggs to two-celled
embryos. Probably most of the eggs were fertilized between 1 and 2 P.M.

Development of the embryo. After fertilization the zygote develops a definite
wall and elongates considerably. Division of the zygote takes place very soon
after fertilization. A number of two-celled embryos were found at 2 P.M. three
hours after the first sperms were observed in the embryo sacs. The first wall is
transverse. This wall cuts off a terminal cell from which develop the cotyledons

and epicotyl, as well as a lower cell which gives rise to the hypocotyledonary parts of the embryo. Both cells of the two-celled embryo divide at very nearly the same time. Usually the division of the basal cell lags slightly behind that of the terminal cell. The terminal cell divides by a longitudinal wall and the lower by a transverse wall to form the four-celled embryo. Four-celled embryos were found 6 to 7 hours after fertilization. Every cell of the four-celled embryo contributes to the formation of the eight-celled embryo. Again, each tier of cells usually divides slightly in advance of the one below it. Eight-celled embryos were observed in samples collected 20 hours after pollination. The sixteen-celled embryo is formed by the division of each cell of the eight-celled embryo. In the sixteen-celled embryo as many cells have been derived from the basal as from the terminal cell of the two-celled embryo. At this stage there are five tiers of cells. The upper tier of eight cells contributes the cotyledons and plumule. The second tier of four cells gives rise to all the primary tissue of the hypocotyl and the plerome initials; the third tier of two cells produces dermatogen cells and periblem initials. The fourth tier (one-celled) contributes the dermatogen initials and a portion of the root cap, while the fifth tier (also one-celled) develops into a many-celled filamentous suspenser. Cells of the root cap are formed by periclinal division of the cells of the dermatogen.

Endosperm. It appears that there is a simultaneous fusion of the sperm and the two polar nuclei to form the primary endosperm nucleus. The divisions of the endosperm nuclei are at first slightly in advance of those of the embryo.

When the embryo is four-celled the endosperm nuclei have almost completed their fourth division. During the early stages, the divisions of the free nuclei are usually nearly simultaneous. This parallelism of division, however, is not always maintained. By the time the eight-celled embryo is formed, twenty hours after pollination, walls have appeared in the endosperm, The endosperm cells at this time completely fill the embryo sac; they are few in number, very large and highly vacuolate. The endosperm cells divide and for a considerable time continue to occupy the space within the rapidly growing embryo sac. The developing embryo rapidly encroaches upon the endosperm digesting and absorbing it. By the seventh day after pollination the endosperm tissue is almost entirely destroyed. The walls of the two outer cell layers of the endosperm become somewhat thickened and are very conspicous during the late stages of seed development. The membrane thus formed is present in the ripe seed and completely invests the embryo.

The endosperm cells do not contain much reserve food at any stage of their development. When the seed is ripe all of the reserve food is stored within the cells of the embryo, and it is upon this food supply that the growing seedling must subsist until it starts to manufacture its own food supply.

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EFFECT OF LENGTH OF DAY ON GROWTH AND DEVELOPMENT OF PLANTS[1]

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INTRODUCTION

In a series of articles beginning in 1920 Mr. H. A. Allard and the writer have presented considerable experimental evidence tending to show that the relative length of day and night is an important factor in the growth and development of many plants. It has been shown that in many cases flowering and fruiting and other features of plant activity may be controlled to a surprising degree by suitable regulation of the daily illumination period. To designate the response of the plant to relative length of day and night, the term "photoperiodism" has been suggested. Early in these investigations it became apparent that: (1) species and varieties differ widely in their requirements as to length of day, for maximum response in a given direction; (2) species and varieties also differ markedly in their sensitiveness to this factor. Thus, flowering may be induced in some plants by exposure to a relatively short day, while in other plants flowering is favored by a relatively long day, and in still others, flowering readily occurs under either a long or a short day and even under continuous illumination.

The method of experimentation followed is very simple. During the open growing season the number of hours of daily illumination received by the plants is regulated by keeping them in light-proof, ventilated houses during the early morning or late afternoon, or both. To facilitate the daily transfer, steel tracks leading into the dark house were provided, and on these tracks were placed a number of trucks arranged for supporting the plants in their containers. The duration of the tests in the open is limited, of course, by the natural shortening of the daylight period, and by the advent of cold weather as summer gives way to fall. During the winter months the experiments are conducted in a green-house provided with electric illumination to supplement daylight, in order to prolong the daily period of illumination. During both summer and winter control plants are exposed to the full natural daylight period. On the whole very satisfactory results have been obtained by these methods. These results are being checked and somewhat elaborated, however, by supplementary tests in which conditions of illumination and temperature are more accurately controlled.

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug. 19, 1926.

SHORT-DAY PLANTS AND LONG-DAY PLANTS

There are many species and varieties which are vigorously vegetative and rapidly increase their stature when exposed to a relatively long day-length, such as prevails during the midsummer period in the temperate zone, but flower readily when exposed to a relatively *short length* of day such as occurs in late summer and fall. Both annuals and perrennials are found in this group. Thus, plants normally flowering in late summer or fall or in early spring may be caused to flower in early summer by appropriately shortening the daylight period. Conspicuous examples are the Biloxi variety of soybean, *Cosmos sulphureus* L, *Perilla frutescens* (L.) Britton, *Aster linariifolius* L, *Tithonia rotundifolia* (Mill) Blake, Poinsettia, and *Viola papilionacea* Pursh. In plants of this group there appears to be an optimal light period for flowering which varies with the species and variety but for a number of plants seems to be in the neighborhood of 10 hours. Flowering usually occurs more or less readily, however, over a considerable range on either side of the optimal light period. Within this range, so far as has been observed, the height attained by the plant at time of flowering usually decreases with decrease in the light period.

It has been found that there is another large group of plants which flower most readily when exposed to a relatively *long daylight period*, such as occurs from late spring through midsummer in extra-equatorial regions. Exposure to a short day length commonly delays elongation of the axis in this group of plants. Numerous biennials as well as annuals and perennials belong in this group. Examples are red clover, *Oenothera biennis* L; *Rumex acetosella* L; *Rudbeckia bicolor* Nutt., *Sedum Stahlii* L; and the sugar beet. In some plants of this group there is apparently an optimal light period for flowering and an illumination period in excess of the optimal may be injurious or even fatal. Other members of the group, however, may flower most readily with continuous illumination, at least with the mazda lamp as the light source. In this group as a whole the height of the axis at time of flowering usually increases with increase of the light period up to and somewhat beyond the optimal for flowering.

For convenience, plants flowering in response to a short day have been designated as "short-day plants" and those responding to a long day have been called "long-day plants." This classification while useful is more or less arbitary, since no hard and fast line can be drawn between the two classes of plants.

Some plants are not particularly sensitive to the light period with respect to time of flowering, although they may be otherwise affected. Among these are plants which flower through a very wide range in length of day and in such plants the *height attained* usually *increases* with *increase in day length*. Moreover, some plants might be classed as long-day at a latitude having a maximum day length of, say, 15 hours while at a latitude with a maximum day length of, say, 17 hours they would show the typical short-day response. It is probably significant, however, that among the more typical short-day plants are found those that regularly show more or less development of the primary axis under all day lengths and even in continuous darkness. On the other hand, the typical long-day group includes those that elongate the axis with difficulty if at all when exposed

to a short day length. Many members of both the short-day and long-day groups are only moderately delayed in flowering by intermediate day lengths, although, of course, these day lengths are above the optimal for the former and below the optimal for the latter group.

Some Special Features of Photoperiodism

Exposure to a suitable light period tends to induce the everblooming type of expression. Thus with the short-day plants flowering is favored by a short day while a long day favors vigorous vegetative growth. It is not surprising, perhaps, to find that a light period between the two extremes is favorable to a combination of both the vegetative and reproductive forms of activity and, therefore, may cause plants of this type to behave as ever-bloomers. Under these conditions such plants may continue to manifest the everblooming characteristic for a prolonged period.

An interesting fact developed in the early stages of our investigations is that darkening plants in the middle of the day is largely without effect in most cases so far as concerns flowering. In this respect most plants thus darkened behave much the same as when exposed to the full daylight period. For example, a reduction of 65 per cent in the total light energy received by the plants by darkening during the middle of the day was less effective in hastening flowering in certain varieties of soybean than was a reduction of $2\frac{1}{2}$ per cent in total light energy by excluding the early morning daylight. In this case the mid-day darkening period was 6 hours while the early-morning darkening period averaged about 40 minutes. Obviously the continuity of the light period as well as the total number of hours of light received daily by the plant may have an important effect on the length of the vegetative period.

Evidence has been obtained indicating that when late-flowering Cosmos is abruptly transferred from a long to a short day, laying down of flower primordia begins within 3 to 5 days and by the end of 10 days flower buds are visible to the naked eye. If the plant is returned to long-day conditions before the expiration of about 10 days, further development of flower buds is arrested and vegetative growth is soon resumed. If the plant is allowed to unfold its blossoms before it is restored to the long day, seed formation may be completed and adjoining plant parts pass into senescence and finally die. Subsequently, however, vigorous new shoots develop in response to the longer light period and the life of the plant is thus maintained for a prolonged period. In this way typical annuals may be caused to resemble in a measure the behavior of perennials. The new growth primarily is strongly vegetative but commonly is accompanied by occasional flowering, indicating that the flowering condition, once it has been induced, is completely destroyed only with difficulty.

As bearing on the action of the light period it is worthy of mention that with many plants the use of artificial light of intensity as low as 5 or 10 foot candles to lengthen the daily illumination period by supplementing the short daylight period of winter may give essentially the same formative effects as

are produced by daylight alone during the long days of summer. By this method flowering is greatly delayed in short-day plants and is correspondingly hastened in long-day plants. On the other hand, it appears that the general nutrition of the plant is not fully maintained by the partial substitution of weak artificial light for sunlight.

It has been found that under suitable conditions the response to length of day may be rather sharply localized in the plant. If one of two coordinate branches of late-flowering Cosmos is exposed to a 10-hour day while the other is exposed to a 16-hour day, the former promptly flowers and develops seeds, while the latter continues to grow vigorously without flowering. Again, if the lower portion of the primary axis of *Cosmos sulphureus* is exposed to a day length of 10 hours, while the upper portion is exposed to the full length of day of summer, the former soon flowers while the latter remains vegetative. When the central portion of the axis is exposed to a long day while both the lower and upper-most portions are subjected to a short day, flowering takes place in both the latter portions of the axis while the central portion develops only vegetative shoots.

INCREASE IN STATURE AND TUBERIZATION

Under conditions otherwise favorable the light period may have a marked effect on rate of increase in stature and final height attained, whether or not flowering is involved. Reference has already been made to the relation of the light period to increase in height of plants within the limits favorable to flowering. In the case of the short-day type of plant, elongation of the axis continues for long periods when the day length is excessive with respect to flowering, and under these circumstances the plant may become abnormally tall. Just how long this type of vegetative activity may continue has not been determined, although plants having a vegetative period of only a few weeks under a short day have continued to increase in stature without flowering for 18 to 24 months under a long day, which is as far as the experiment has been carried. The rate of the increase in height in relation to the light period has not been fully determined, but the indications are that in some plants of the short day type there is an optimal light period for rate of increase in stature, while it is possible that some plants of this group may increase in height most rapidly under continuous illumination.

In the case of woody perennials which have not attained the flowering stage marked differences have been observed in the effect of long and short days on the growth rate. Seedlings of *Acer negundo* were found to grow more rapidly under a 15-hour day than under a 10-hour day, while young apple trees grew more rapidly under the short day.

With respect to annuals and herbaceous perennials of the long-day class a short day exposure tends to delay or inhibit elongation of the axis. Vegetative activity may continue for long periods under these conditions. Frequently this form of activity is accompanied by tuberization, apparently indicating accumu-

lation of carbohydrate which, under the conditions, cannot be used in stem development. Formation of tubers also frequently occurs when the light period is long enough to allow considerable stem elongation. As far as our observations extend, however, tuberization is usually favored by relatively short days. On the other hand, in the onion vegetative activity is favored by a relatively short day while a long day favors bulb formation.

Ecological Significance of Length of Day

A great deal of work must be done before the exact significance of length of day in plant behavior can be determined. The response of the plant to this factor is, of course, influenced by various other factors of the environment. Since the relative length of day and night varies with the latitude and with the season it may be inferred from the facts already developed that this factor has definite bearing on plant behavior at different latitudes and at different seasons of the year. In general, mean temperature also varies with latitude and season and there is probably an important interrelationship of length of day and temperature as factors in the distribution of plants and in their seasonal behavior. As suggestive of this interrelationship, mention may be made of observations on soybean and the beet, two crop plants differing in their requirements both as to length of day and temperature.

Certain early, medium, and late varieties of soybean have been studied in considerable detail. At Washinton field plantings of the Mandarin, Peking, Tokio, and Biloxi varieties, which germinate during the latter part of May, show vegetative periods of approximately 4 weeks, 8 weeks, 10 weeks, and 14 weeks, respectively. Plantings made later and later in the season show a progressive decrease in length of the vegetative period, the reduction being greatest in the latest variety, so that with advance of season the vegetative periods of the four varieties tend to become the same. When exposed to a 10-hour day in summer the vegetative period of all the four varieties is reduced to somewhat less than 4 weeks. The June length of day seems to be only slightly in excess of the optimal light period for flowering in the Mandarin, while the other varieties require progressively shorter light periods. Plantings over a period of years show that within the range of temperature commonly experienced during the growing season, higher temperatures tend to hasten flowering in all varieties. The evidence indicates that differences between the early and late varieties in time of flowering is due primarily to their specific light requirements while the actual date of flowering of any particualr variety is also influenced by temperature. With conditions otherwise favorable to growth it would seem that the ability of a given variety to mature in higher latitudes will depend largely on whether its light period is such that reproductive activities are initiated sufficiently in advance of the arrival of cold weather and is subject also to the retarding action of relatively low summer temperatures.

The common table beet is ordinarily a biennial in this region. It belongs to the long-day class of plants and even in the second year flowers only with

difficulty when exposed to a short day. It is known, also, that exposure to warm temperatures during the winter may prevent flowering in the second year. At only moderately high latitudes and at low altitudes the long days of summer are usually associated with high temperatures and under these circumstances the beet requires two seasons for completing the life cycle. It has been found experimentally, however, that when subjected to the combination of a long day and a cool temperature such as would be found in very high latitudes, the beet may become an annual.

THE INFLUENCE OF SHADE ON THE BEHAVIOR OF APPLE TREES[1]

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INTRODUCTION

The deleterious effect of shade on the growth and fruiting of apple trees is well recognized. In fact its recognition, particularly in old trees, is emphasized in our pruning recommendations, which lay stress on the necessity of opening up the trees to admit light, which is one of the factors influencing spur growth, fruit bud formation, and color of fruit. The lower limbs, especially of old trees, and crowded trees, become poorly vegetative and non-fruitful.

Since poorly vegetative and non-fruitful conditions have been associated with certain changes in chemical composition, however induced, it would seem probable that shaded portions of an apple tree would show a chemical composition which is associated with poor growth and non-fruitfulness, probably a certain carbohydrate nitrogen relationship. Kraybill ('23) has already pointed out that after two years of shading whole trees of apple and peach, the carbohydrate nitrogen relation was changed. The inhibition of blossoming and growth responses of these trees were previously noted by Gourley ('20).

Shading experiments and length of day studies have been carried on at College Park since 1922. The extensive nature of these experiments has made it seem desirable to make separate reports on some phases of the work. One preliminary report has been made (Auchter and Harley '24) on length of day studies with soybeans, lettuce, and peppers. The present report includes shading studies with Steyman Winesap and Grimes Golden apple trees of bearing age (12 to 14 years).

OUTLINE OF EXPERIMENTS

During 1922 and 1923 shading of whole trees was done, using one Grimes Golden and three Stayman Winesap trees. The same trees were shaded both years. One tree of each variety was used as a check, one Grimes Golden tree and two Stayman Winesap trees were shaded only five weeks in the spring of 1922, and again in 1923, commencing just before blossoming and ending about May 15th. One Stayman Winesap tree was shaded during the full seasons of 1922 and 1923.

[1] Presented before the International Congress of Plant Sciences, Section of Horticulture, Ithaca, New York, Aug 19, 1926. Some of the data contained in this paper were secured by Messrs. F. S. Lagasse and W. W. Aldrich while taking graduate work at the University of Maryland.

After noting the marked effects of shading whole trees, the question arose as to whether shading half a tree would result in the same responses, or if the unshaded half would influence the response of the shaded half, possibly by cross-transfer of carbohydrates, or by any other means. Accordingly, two Stayman Winesap trees and two Grimes Golden trees were selected in the spring of 1924, the limbs of which were distributed so that a muslin shade could be placed conveniently over one side of the tree (Fig. 1).
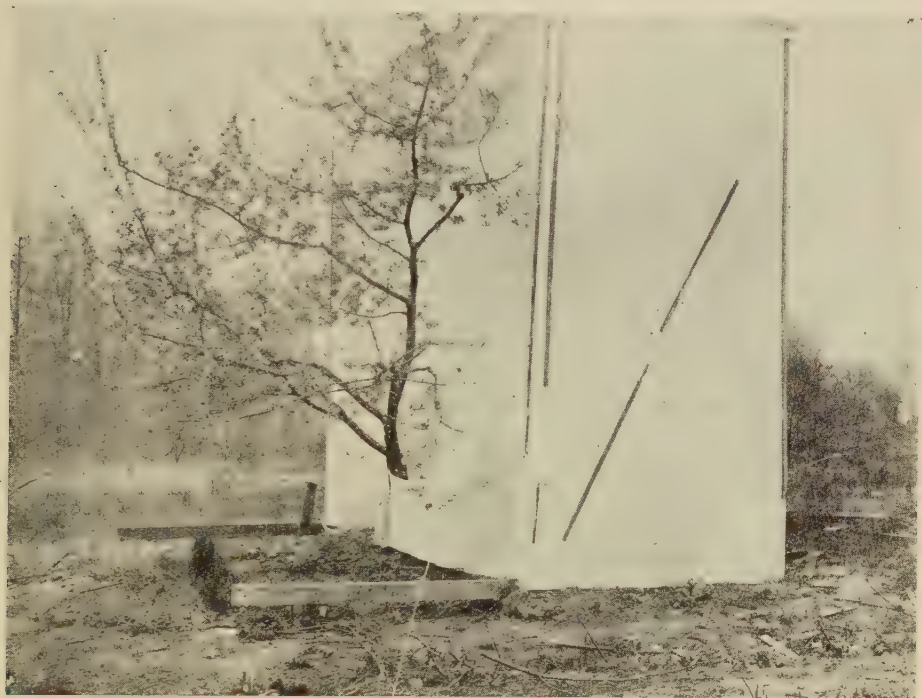
Fig. 1. Showing kind of muslin tent used to shade halves of Grimes Golden and Stayman Winesap tree. Provision was made for air circulation after pollination time.

Shading was accomplished by means of muslin tents which were erected by building wooden frames over the trees to support the muslin. The relative intensity of the light under such tents as compared to outside conditions was found to be $N/19.6$ as measured by a Bee exposure meter. In the shading experiments by Gourley ('20) a relative intensity of $N/6.15$ was measured under the shade employed at New Hampshire. Thus, it can be seen that the intensity of the light in Maryland shading work was less than that used at New Hampshire.

METHODS OF CHEMICAL ANALYSIS

Samples taken on June 26th, 1924, October 4th, 1924, and April 1st, 1925 were dried directly in an oven at 80°C. The remaining samples on June 25th, 1925, and August 27th, 1925, were placed in hot alcohol and refluxed for one hour.

The spur samples consisted of fifty spurs each and the terminal samples consisted of twenty terminals each. Care was taken to have uniform lengths of growth.

Extraction. An oven dried aliquot of dry material, ground to pass a forty mesh screen, was extracted for three hours in a Soxhlet siphon extractor, using 50 per cent alcohol in the extraction flask.

Free reducing substances. The alcohol was driven off from the extract on a water bath, and water added. Clearing was done with neutral lead acetate, and deleading was done by means of anhydrous sodium carbonate. The reducing power was determined by the Bertrand modification of the Munson-Walker method. The results are reported as dextrose.

Total sugars. An aliquot of the cleared extract was hydrolyzed with 5 cc of concentrated hydrochloric acid (sp gr 1.125) at room temperature for twenty-four hours, neutralized with anhydrous sodium carbonate, and the reducing power determined. The results are reported as dextrose.

Acid hydrolyzable materials. An aliquot of the residue from the sugar extraction was hydrolyzed by boiling in a hydrochloric acid solution (10 cc of concentrated acid to 100 cc of water) for two and one-half hours. Anhydrous sodium carbonate was used to neutralize. The reducing power was determined of the filtered solution. The results are reported as dextrose.

Starch. An aliquot of the residue from the sugar extraction was ground to a fine powder, adding white quartz sand to facilitate grinding. A saliva digestion for two periods, the first of one hour and the second of thirty minutes sufficed to convert all starch in the tissue. Removal of interfering polysaccharides was then accomplished by alcoholic precipitation as recommended by Walton and Coe ('23). After removal of the alcohol on a water bath, hydrolysis of the solution by boiling with 10 per cent hydrochloric acid for two and one-halfh ours was done. Neutralization was made with anhydrous sodium carbonate, and the reducing power determined. The results are reported as dextrose.

Alcohol soluble nitrogen. After eliminating the alcohol and water on a water bath, the residue from an alcoholic extraction as used for sugars was analyzed for nitrogen by the Jodlbauer-Forster modification of the Gunning-Kjeldahl method.

Alcohol insoluble nitrogen. The nitrogen in the dried residue from the alcoholic extraction was determined by the above method.

Total nitrogen. Total nitrogen was computed from the results of soluble and insoluble nitrogen.

RESULTS OF SHADING WHOLE TREES—1922–1923

Effect on foliage. The leaves on the shaded trees were larger but much thinner than leaves of adjacent unshaded trees. The area of the average leaf from Stayman Winesap trees shaded all season was seventy-two per cent greater than the average area of leaves of unshaded trees. An examination of the leaf structure of shaded leaves showed a reduction of the number of palisade cells and spongy parenchyma tissue. Hence, although of greater area, the shaded leaves

had less dry matter than unshaded leaves. These observations are in accordance with those of Gourley ('20). Trees which were shaded only for the first five weeks of the growing season showed similar effects on the foliage although less marked.

It was noted that leaf fall occurred about two weeks earlier with the trees shaded all season.

Effect on terminal growth. Shaded trees produced a longer and more slender type of growth which did not mature or ripen, but was greenish and pubescent at the end of the season as compared with the dark brown wood of unshaded trees. Much winter injury of spurs and terminals resulted from lack of maturity of the growth of shaded trees, especially on the lower limbs. In 1922 the

Fig. 2. Leaf development on Apr. 26, 1924, unshaded Stayman Winesap tree. Compare with Figure 1.

average terminal growth of shaded Stayman Winesap trees was 11.19 inches as compared with 6.88 inches for the unshaded trees. In 1923 an average terminal growth of 9.34 inches was obtained from the shaded trees while an average of only 6.11 inches of terminal growth occurred on the unshaded trees. The diameters of these terminal growths in 1923 was as follows: (1) Shaded terminals at base 0.13 inches and at tip 0.07 inches. (2) Unshaded terminals at base 0.19 inches and at tip 0.13 inches. These measurements on two hundred terminals in 1922 and one hundred and twenty-five terminals in 1923 show clearly that shading induced a longer, more slender terminal growth. The internodes of such terminals were 20 per cent longer than internodes of unshaded terminals.

A very peculiar growth response was noted in that the terminals and older branches made a curled and twisted growth often turning at sharp angles.

Effect on spur growth. Spur growth on the shaded tree was more slender, and many of the spurs on the lower branches died. After two years shading, the shaded spurs (May 1924) had an average of only 3.17 leaves per spur compared to 8.92 leaves on the unshaded spurs on Stayman Winesap trees.

Effect on starting of buds in spring. It is interesting to note that the shaded trees were five days later in starting in the spring of 1924 following two years of shading. Compare Figures 2 and 3.

Fig. 3. Leaf development on Apr. 26, 1924. Stayman Winesap tree shaded during the two previous seasons. Note delayed development as compared with Figure 1.

Effect on blossom bud formation. The shading during the first season (1922) practically prevented any blossom bud formation, even though no crop was produced in 1922, and during the second season of shading (1923) not a blossom formed. Even five weeks of shading in the spring of 1922 seemed to decrease the amount of blossom buds formed and greatly decreased the amount of bloom "set." It will be recalled that the shade on the trees was removed about the middle of May, or about five weeks before differentiation of fruit buds normally occurs in this region. Table 1 gives the blossoming data of the shaded and check trees, according to counts on one thousand spurs over each tree.

Effect on set of fruit. Besides the effect on blossom bud formation, it was noted that the blossoms which were formed on shaded trees were less apt to set fruit than blossoms on unshaded trees. The data on set of fruit taken at the end of May before the June drop, are included in Table 1. The few blossoms oc-

TABLE 1. SHOWING THE EFFECT OF SHADE ON BLOSSOMING AND SET OF FRUIT OF STAYMAN WINESAP AND GRIMES GOLDEN APPLE TREES

Tree	Treatment	1923		1924	
		Per cent spurs blos.	Percent set of blos. spurs	Per cent spurs blos.	Per cent set of blos. spurs
Stayman Winesap 1.	Check	44.0	33.6	90.1	20.0
Stayman Winesap 2.	Shaded all season in 1922 and 1923	1.4	0	0	0
Stayman Winesap 3.	Shaded 5 weeks Spring 1922 and 1923	25.0	0	18.2	10.0
Stayman Winesap 4.	Shaded 5 weeks Spring 1922 and 1923	32.7	0.4	40.0	5.0
Grimes Golden 1.	Shaded 5 weeks Spring 1922 and 1923	17.2	0	25.0	24.8
Grimes Golden 2.	Check—no shade	57.0	6.6	18.2	30.2

NOTE: Blossoming branches of Grimes Golden and hives of bees were placed under the shaded Stayman Winesap trees to provide for cross-pollination of this self-sterile variety.

curring in 1923 on the Stayman Winesap tree (shaded all season of 1922) did not set a single fruit. One Stayman Winesap and one Grimes Golden tree shaded for five weeks in 1922 and 1923, failed to set a fruit in 1923 although blossoming moderately well. This effect on set of fruit though not so marked, can also be seen in the 1924 records. Morris and Luce ('26) report a decreased set of blossoms on lower limbs of trees in a crowded orchard, largely due to shading effects.

Effect on chemical composition. Microchemical tests for starch which were made on terminals and spurs of Stayman Winesap, on April 2, 1924, after two years of shading indicated a very low starch content in the shaded tree as compared to the unshaded tree. Samples of non-blossoming spurs were taken at several dates during the two years of shading but have not as yet been analyzed.

RESULTS OF SHADING HALVES OF TREES—1924–1925

The growth responses of halves of trees under shade were similar to those of whole trees in many respects, that is, large, thin leaves, curling of limbs, and a *thin spindly type of spur and terminal growth.* However, the terminal growth, although longer on the shaded halves than on the unshaded halves, in the first season, was distinctly shorter in the second season of shading. The condition of shorter terminals in the second season agrees with numerous observa-

tions of poor growth on shaded limbs of dense trees. This decrease of the shaded side as compared to the unshaded side during the second year, which was not noted when whole trees were shaded is, no doubt, due to some effect of the

TABLE 2. SHOWING THE EFFECT OF SHADING HALVES OF STAYMAN WINESAP AND GRIMES GOLDEN APPLE TREES, SHADED IN 1924 AND 1925

Tree	Per cent spurs blossoming 1925		Per cent of spurs blossoming 1926	
	Unshaded half	Shaded half	Unshaded half	Shaded half
Stayman 1,	0*	0	49	2
Stayman 2,	0*	0	80	7
Grimes 1,	0*	0	47	9
Grimes 2,	0*	0	45	0

* These unshaded halves bore a crop in 1924 which explains the lack of blossoming in 1925. The shaded halves did not bear a crop in 1924 and did not form blossom buds for 1925 either.

unshaded half, possibly on the water supply. Water relations could easily be disturbed, since the cross transfer of water in woody plants has been shown to occur by Auchter ('23).

TABLE 3. ANALYSES OF NON-BEARING SPURS FROM SHADED HALVES AND UNSHADED HALVES OF GRIMES GOLDEN AND STAYMAN WINESAP TREES, SAMPLED ON JUNE 26TH, 1924 IN THE FIRST SEASON OF SHADING

Expressed in per cent of dry weight

Tree	Treatment	Dry Matter	Free Reducing substance	Total sugars	Acid Hydro-lyzable Poly-saccharides	Starch
Stayman I	Unshaded half	34.55	1.78	1.83	19.58	2.93
	Shaded half	31.10	2.04	3.04	18.25	2.85
Stayman II	Unshaded half	34.33	0.705	1.41	17.18	4.77
	Shaded half	28.65	0.795	1.33	16.16	2.05
Grimes I	Unshaded half	37.90	2.20	3.94	22.73	3.29
	Shaded half	32.00	1.95	2.90	22.92	3.79
Grimes I	Unshaded half	39.15	2.04	2.71	23.82	3.80
	Shaded half	23.75	1.56	2.73	21.67	3.64

Expressed in absolute amounts (milligrams) per spur

Tree	Treatment	Dry Matter	Free Reducing substance	Total sugars	Acid Hydro-lyzable Poly-saccharides	Starch
Stayman I	Unshaded half	42.7	0.76	0.78	8.36	1.25
	Shaded half	36.8	0.75	1.12	6.72	1.05
Stayman II	Unshaded half	62.4	0.44	0.88	10.72	2.98
	Shaded half	46.5	0.37	0.62	7.52	0.95
Grimes I	Unshaded half	35.5	0.78	1.40	8.08	1.17
	Shaded half	26.4	0.51	0.77	6.06	1.00
Grimes II	Unshaded half	48.7	0.99	1.32	11.50	1.85
	Shaded half	25.7	0.40	0.70	5.56	0.93

TABLE 4. ANALYSES OF TERMINAL GROWTHS FROM SHADED HALVES AND UNSHADED HALVES OF GRIMES GOLDEN AND STAYMAN WINESAP TREES, SAMPLED ON OCTOBER 4, 1924, AFTER THE FIRST SEASON OF SHADING.

Expressed in per cent of dry weight

Tree	Treatment	Dry Matter	Free reducing substance	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	50.95	1.53	1.73	33.22	10.15	0.265?	0.070	0.195
	Shaded half	45.25	1.83	2.02	30.92	8.50	0.745	0.159	0.586
Stayman II	Unshaded half	53.22	1.53	1.58	48.46	11.79	0.552	0.056	0.496
	Shaded half	44.25	1.49	1.96	32.13	10.71	0.807	0.138	0.669
Grimes I	Unshaded half	53.39	1.29	1.61	31.48	10.14	0.755	0.118	0.637
	Shaded half	49.65	1.26	1.59	32.67	10.52	0.814	0.125	0.689
Grimes II	Unshaded half	53.41	1.64	2.55	34.85	11.28	0.720	0.097	0.623
	Shaded half	53.64	2.57	3.31	33.30	10.77	0.672	0.104	0.568
Grimes Check No shade	North-half	51.10	0.709	1.22	32.28	9.83	0.771	0.138	0.633
	South-half	51.95	0.682	1.21	33.81	9.92	0.806	0.118	0.688

Expressed in absolute amounts (milligrams) per terminal

Tree	Treatment	Dry Matter	Free reducing substance	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	832.0	12.7	14.4	276.4	84.4	2.20	0.58	1.62
	Shaded half	622.8	11.4	12.6	192.6	52.9	4.64	0.99	3.57
Stayman II	Unshaded half	557.8	8.53	8.81	270.3	65.8	3.08	0.31	2.77
	Shaded half	353.5	5.27	6.93	113.3	37.9	2.85	0.49	2.36
Grimes I	Unshaded half	547.3	7.06	8.81	172.3	55.5	4.13	0.65	3.48
	Shaded half	483.3	7.06	7.68	157.8	50.8	3.94	0.61	3.33
Grimes II	Unshaded half	651.2	10.6	16.7	227.0	73.4	4.69	0.63	4.06
	Shaded half	411.0	10.5	13.6	136.8	44.3	2.76	0.43	2.33
Grimes Check Unshaded	North-half	613.3	4.35	7.31	198.6	60.3	4.73	0.85	3.88
	South-half	571.5	3.90	6.91	193.2	56.7	4.61	0.67	3.93

TABLE 5. ANALYSES OF TERMINAL GROWTHS FROM SHADED AND UNSHADED HALVES OF GRIMES GOLDEN AND STAYMAN WINESAP TREES, SAMPLED ON APRIL 1, 1925, AFTER ONE YEAR OF SHADING

Expressed in per cent of dry weight

Tree	Treatment	Free reducing substance	Dry Matter	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	3.52	47.95	5.10	29.58	9.13	0.776	0.118	0.658
	Shaded half	4.21	45.90	5.45	26.80	4.92	0.895	0.191	0.704
Stayman II	Unshaded half	2.63	48.40	3.17	31.02	7.14	0.825	0.152	0.673
	Shaded half	4.05	46.65	5.30	26.15	6.51	0.926	0.174	0.752
Grimes I	Unshaded half	2.50	47.82	2.72	29.06	6.45	0.852	0.125	0.727
	Shaded half	0.72	42.95	1.38	31.58	4.51	0.272?	0.125	0.148
Grimes II	Unshaded half	1.46	47.41	1.88	29.60	7.15	0.808	0.285	0.523
	Shaded half	2.45	43.22	2.91	27.81	6.47	0.857	0.184	0.673

Expressed in absolute amounts (milligrams) per terminal

Tree	Treatment	Free reducing substance	Dry Matter	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded ha f	16.0	454.5	23.2	134.5	41.5	3.53	0.54	2.99
	Shaded half	19.5	462.8	25.2	124.0	22.8	4.14	0.88	3.26
Stayman II	Unshaded half	16.6	632.8	20.1	196.3	45.2	5.22	0.96	4.26
	Shaded half	18.8	464.8	24.6	121.5	30.3	4.31	0.81	3.50
Grimes I	Unshaded half	20.6	825.8	22.5	240.0	53.3	7.03	1.03	6.00
	Shaded half	3.9	543.8	7.50	171.7	24.5	1.48	0.68	0.80
Grimes II	Unshaded half	15.9	1087.5	21.9	345.0	83.3	9.42	3.32	6.10
	Shaded half	16.5	675.3	19.6	187.8	43.7	5.74	1.24	4.54

TABLE 6.   ANALYSES OF TERMINAL GROWTHS FROM SHADED AND UNSHADED HALVES OF GRIMES GOLDEN AND STAYMAN WINESAP TREES, SAMPLED ON JUNE 25TH, 1925, IN THE SECOND SEASON OF SHADING

Expressed in per cent of dry weight

Tree	Treatment	Free reducing substance	Dry Matter	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	2.59	46.70	3.51	28.73	2.04	0.664	0.142	0.522
	Shaded half	2.71	45.46	3.74	28.78	2.23	0.698	0.186	0.512
Stayman II	Unshaded half	2.35	52.55	2.99	28.72	1.52	0.947	0.317	0.630
	Shaded half	2.60	48.35	3.20	28.62	1.64	0.696	0.152	0.544
Grimes I	Unshaded half	1.81	46.25	2.50	30.10	2.56	0.843	0.238	0.605
	Shaded half	2.34	46.35	3.07	30.65	2.96	0.877	0.258	0.619
Grimes II	Unshaded half	1.94	45.79	2.74	30.25	2.41	0.774	0.171	0.603
	Shaded half	1.60	48.00	2.13	30.76	2.09	0.674	0.154	0.520
Grimes Check Unshaded	North-half	2.17	47.70	2.87	30.00	2.49	0.647	0.104	0.543
	South-half	2.19	51.30	3.09	31.01	2.81	0.608	0.080	0.528

Expressed in absolute amounts (milligrams) per terminal

Tree	Treatment	Free reducing substance	Dry Matter	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	25.4	980.0	34.4	281.6	20.0	6.51	1.39	5.12
	Shaded half	18.9	700.3	26.2	201.6	15.6	4.89	1.30	3.59
Stayman II	Unshaded half	22.2	944.4	28.2	271.2	14.4	8.94	2.99	5.95
	Shaded half	15.3	586.4	19.3	167.8	9.62	4.08	0.89	3.19
Grimes I	Unshaded half	14.9	820.9	20.5	247.1	21.0	6.92	1.95	6.92
	Shaded half	11.3	483.3	14.8	148.1	14.3	4.24	1.25	4.24
Grimes II	Unshaded half	12.6	650.3	17.8	196.7	15.7	5.03	1.11	3.92
	Shaded half	9.4	587.6	12.5	181.6	12.3	3.97	0.91	3.06
Grimes Check Unshaded	North-half	23.2	1070.7	30.7	306.8	26.7	6.92	1.11	5.81
	South-half	18.6	849.0	26.2	263.2	23.9	5.16	0.68	4.48

TABLE 7. ANALYSES OF TERMINAL GROWTHS FROM SHADED AND UNSHADED HALVES OF GRIMES GOLDEN AND STAYMAN WINESAP TREES. SAMPLED AUGUST 27, 1925, IN THE SECOND SEASON OF SHADING.

Expressed in per cent of dry weight

Tree	Treatment	Dry Matter	Free reducing substance	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded	53.65	0.56	0.79	34.80	10.70	0.645	0.107	0.538
	Shaded	46.95	1.35	2.07	31.94	8.83	0.650	0.083	0.567
Stayman II	Unshaded	52.14	1.13	1.97	30.17	10.77	0.823	0.190	0.633
	Shaded	52.67	1.36	1.95	29.07	5.06	0.974	0.172	0.802
Grimes I	Unshaded	57.17	0.79	1.64	29.43	8.72	0.910	0.169	0.741
	Shaded	54.75	0.94	1.66	30.70	5.30	0.998	0.272	0.726
Grimes II	Unshaded	56.68	0.59	1.69	30.40	15.45	0.737	0.155	0.582
	Shaded	54.75	0.85	1.65	33.40	8.28	0.482	0.125	0.357
Grimes Check Unshaded	North	52.56	0.75	1.52	30.73	7.07	0.720	0.097	0.623
	South	50.61	0.79	1.56	30.51	7.41	0.625	0.111	0.514

Expressed in absolute amounts (milligrams) per terminal

Tree	Treatment	Dry Matter	Free reducing substance	Total Sugars	Acid Hydrolyzable Polysaccharides	Starch	Total Nitrogen	Alcohol Soluble Nitrogen	Alcohol Insoluble Nitrogen
Stayman I	Unshaded half	1438.8	8.0	11.4	500.7	154.0	9.28	1.54	7.74
	Shaded half	849.0	11.5	17.6	271.2	75.0	5.51	0.70	4.81
Stayman II	Unshaded half	760.9	8.6	15.0	229.6	82.0	6.27	1.45	4.82
	Shaded half	420.8	5.7	8.20	122.3	21.3	4.09	0.72	3.37
Grimes I	Unshaded half	695.7	5.5	11.1	204.7	60.7	6.34	1.18	5.16
	Shaded half	463.9	4.4	7.70	142.4	24.6	4.63	1.26	3.37
Grimes II	Unshaded half	932.7	5.5	15.8	283.5	144.0	6.88	1.45	5.43
	Shaded half	499.8	4.2	8.25	167.0	41.4	2.39	0.60	1.79

Effect on blossom bud formation. All trees in this experiment blossomed about 90 per cent in 1924 at the start of the experiment. However, a light frost killed all the blossoms on the shaded halves although not interfering with a good set of fruit on the unshaded halves. Thus, one half of each tree did not bear a crop, but was shaded, while the other half bore a crop but did not have the influence of shade. The result was that blossom bud formation did not occur on either half of the tree, since the trees did not blossom in 1925. In this second season, 1925, very few blossom buds were formed on the shaded halves, although blossom buds were abundant on the unshaded halves, as evidenced by the blossoming in 1926. The data are given in Table 2.

Effect on chemical composition. Samples of spurs were collected on June 26, 1924, in the first season of shading. However, the scarcity of uniform spurs necessitated the use of terminals for further samples, which were taken on October 4th, 1924; April 1st, 1925; June 25th, 1925; and August 27th, 1925.

Terminals were selected of approximately *equal length* from the shaded and unshaded halves of each tree, usually nine to ten inches. However, it will be remembered that the terminals on the shaded side were much more slender. The results of analyses of the above samples are given in Tables 3, 4, 5, 6, and 7.

A survey of these tables shows that no consistently significant differences in the percentages of materials based on dry weight can be noted until the close of the second season of shading (August 27th, 1925). At that time the shaded halves all show a lower percentage of starch. However, it will be remembered that the unshaded halves bore a crop in 1924 while the shaded halves did not, so that the crop may have had such an effect that differences in analyses did not occur which would otherwise have been present, in samples taken on June 26th, 1924, October 4th, 1924, and April 1st, 1925. Since both sides failed to blossom in 1925, the crop of 1924 evidently inhibited blossom bud formation on the unshaded side, while the shade inhibited blossom bud formation on the shaded side. This might indicate a similarity of composition and type of growth. The terminal and spur growth of both sides was slender in 1924, although the shaded growth was more slender and also retarded in maturity or ripening. The retardation of maturity of the shaded growth was reflected in the higher moisture content of the samples from shaded halves.

However, when the analyses are given on the basis of absolute amounts per terminal and per spur (as given in the tables) it can readily be seen that differences exist at each time of analysis between shaded samples and unshaded samples which were not so evident on a percentage basis. These differences are directly related to the thin, spindly type of growth on the shaded halves of the trees. Terminals and spurs were selected of the same length from both sides of the trees, but owing to the more slender type of growth on the shaded side, much less actual materials are to be found in the shaded terminals and spurs. The differences in dry weight per terminal and spur shows that greater amounts of materials were produced in the unshaded growths. In general, it will be noted that at each time of analysis more carbohydrates and more nitrogen is found in the unshaded terminals or spurs, and that this is especially true after two years of shading.

The results suggest that there has been very little if any cross transfer of carbohydrates, which is similar to the results found by Auchter ('23) relative to the lack of cross transfer of mineral nutrients in woody plants. Shading thus has apparently markedly reduced the synthesis of carbohydrates.

The above findings are in general agreement with those of Kraybill ('23) on whole trees, since two years of shading shows a reduction in the percentage of carbohydrates and an increase in percentage of nitrogen, although the nitrogen differences are not as marked or consistent, and are reversed on an absolute basis.

In considering the relation of carbohydrates to nitrogen, for instance, a starch nitrogen ratio, the proportions are quite similar in both the unshaded and shaded spurs and terminals in 1924, although appreciably less absolute amounts of starch and total nitrogen are found in the shaded spurs and terminals. The facts that neither the shaded nor unshaded halves formed blossom buds in 1924 shows an apparent association of similar composition with similar lack of blossom bud formation.

The thin, spindly type of growth with proportionately less elaborated material might also be associated with the lack of blossoming of the shaded half. Roberts ('26) has strongly emphasized the condition of slender terminal and spur growth (in relation to length) as being closely related to unfruitfulness. According to Roberts this slender type of growth may be over-vegetative (such as occurred in the shading of whole trees and in the first year of shading halves of trees), or the growth may be poorly vegetative (such as occurred in the second year of shading halves of trees). In this shading work, it is felt that the thin, spindly-type of growth with relatively low amounts of both carbohydrates and nitrogen presents a condition which is not favorable for blossom bud formation, even though the proportion of carbohydrates and nitrogen might be the same as the proportion found in growths producing blossom buds. Such a condition is presented in the analyses of June 25th, 1925, when the terminals of shaded halves and unshaded halves showed the same percentages, hence the same proportions, of carbohydrates and nitrogen, although much less absolute amounts of these were found in the shaded terminals. However, no blossom buds were formed on the shaded side, in contrast to the many blossom buds on the unshaded side. Later, on August 27th, 1925, the ratio of starch to nitrogen was found to be quite different in the unshaded and shaded terminals, that is, a lower starch nitrogen ratio in the shaded terminals, due largely to a decreased percentage of starch. No doubt, this lack of balance of carbohydrates and nitrogen may have been unfavorable to blossom bud formation late in the season.

In addition to the chemical considerations, we must also add a possibility that morphological differences might play a part in the inhibition of blossom bud formation on shaded trees or portions of trees.

Conclusions

The shading of a whole tree of Stayman Winesap in 1922 and 1923 resulted in the effects enumerated below. (Shading Stayman Winesap and Grimes Golden trees for only five weeks in the spring showed less marked effects.)

1. Larger, thinner leaves with less dry matter than unshaded leaves, and leaf fall two weeks earlier.

2. Longer but more slender terminal growth in both years of shading. Curling and twisting of terminals and older branches. Failure of terminals to mature, with consequent result of winterkilling.

3. More slender spur growth which winterkilled quite badly.

4. Inhibition of blossom bud formation in both years.

5. Delay of five days in starting of buds in the spring after two years of shading.

6. Reduction in percentage set of fruit.

7. Lower starch content in terminals and spurs after two years of shading.

The shading of halves of Stayman Winesap and Grimes Golden apple trees in 1924 and 1925 resulted in the following effects on growth and chemical composition on these shaded halves.

1. Similar effects on growth as were noted with whole trees, except that terminal growth was shorter on the shaded side in the second season.

2. Inhibition of blossom bud formation.

3. Reduction in carbohydrate synthesis. Apparently little if any cross transfer of carbohydrates occurred from the unshaded side.

The lack of blossom bud formation on the shaded halves is probably associated with the thin, spindly type of growth, lack of maturity of the wood, and the relatively low amounts of carbohydrates and nitrogen in this type of growth. The above effects noted under shade have been observed in a moderate degree on lower limbs and in the centers of dense trees, particularly older trees that have not been pruned. Morris and Luce ('26) in a study of orchard crowding state that shading of the lower limbs due to crowding caused a weak spur growth on the lower limbs and slender upright branch growth in the top with few wide spurs, or fruiting branches. The bad effects of shade on growth and fruitfulness, as well as on color of fruit, emphasizes the need to regulate our pruning and planting practices with light as one of the main considerations.

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INFLUENCE OF TEMPERATURE ON FLOWERING IN CELERY[1]

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This paper summarizes results of one phase of a general study of flowering and seeding of celery, which has been carried on at Ithaca during the past seven years. Of the various environmental factors influencing seeding of celery, temperature seems to have the most marked effect. Exposing the young plants to relatively low temperature in the cold frame (above freezing) for periods of from 15 to 35 days has resulted in the production of flowers and seed the first year. Similar lots of plants kept in the greenhouse at an average temperature of 60°F. until time for planting in the field did not produce flowers. Results of other experiments carried on in the greenhouse, where the plants were grown to maturity, indicate that relatively high temperature, averaging 70° F., prevented seeding regardless of the previous treatment. High temperature favored vegetative growth and prevented reproduction. If, however, flower stalks had started before the plants were subjected to high temperature, flowering and seeding were hastened by the transfer from low or medium to high temperature.

The results obtained in these experiments explain why celery plants sometimes go to seed the first year while at other times they do not.

Chemical studies are being made to determine whether or not there is any definite correlation between the composition of the plants and their observed behavior.

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THE PHYSIOLOGICAL SIGNIFICANCE OF CARBOHYDRATE ACCUMULATION[1]

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The formation of blossom buds in the apple is associated with the accumulation of carbohydrate in the vicinity of the bud at the beginning of the period of bud differentiation. Since this paper is an investigation into the signifiance of this association, the original evidence therefore will first be reviewed (Hooker '20). On June 26, 1919, seven samples of apple spurs were collected in central Missouri and were subjected to chemical analysis. Three of these samples comprised the one-year-old wood and the new growth from bearing spurs of Wealthy, Ben Davis, and Jonathan trees. The Wealthy and Ben Davis trees were biennial in their bearing habit, the Jonathan was a regular, annual producer. Two samples comprised the one-year-old wood and the new growth from non-bearing spurs of Ben Davis and Jonathan trees, the former being in the off year of biennial bearing and the latter being the same tree from which bearing spurs were collected. Two samples consisted of unproductive spurs from Ben Davis and Nixonite trees that had never borne even a moderate crop of fruit and were considered barren.

The first question that presents itself in connection with these samples concerns the percentage of spurs in each sample that formed blossom buds. This point had not been determined at the time the original data were published. To remedy this omission the spur performance of the trees that were sampled has since been studied. On the basis of this study the percentage of blossom bud formation on the bearing spurs may be considered to be nil, the small percentage of consecutive blossoming found on these trees being confined in all probability to spurs that failed to set fruit. In the samples of non-bearing spurs the percentage of blossom bud formation as indicated by the spur record of 1919 for spurs of the type sampled, was 68 per cent for the Jonathan and 89 per cent for the Ben Davis. These two samples were truly representative of spurs that form blossom buds. The percentage of blossom bud differentiation among the barren spurs was 1.3 per cent for the Ben Davis tree and 2.8 per cent for a Nixonite tree standing next to the one sampled.

The chemical analyses showed that the bearing spurs contained very little starch and a moderate percentage of nitrogen. The non-bearing spurs contained somewhat less nitrogen and appreciable amounts of starch. It is interesting to note that the higher percentage of starch was found in the sample of non-bearing

spurs from the Ben Davis tree on which a somewhat higher percentage of the non-bearing spurs formed blossom buds. The barren spurs, less than 3 per cent of which formed blossom buds, according to the record of spur performance, contained approximately as little nitrogen as the non-bearing spurs and no more starch than the bearing spurs.

Similar results were obtained in 1920 with York trees in the "on" and in the "off" year (Hooker '22). The percentage of starch found in bearing spurs on June 19 was less than 9.36 per cent in all of the four samples taken. Two samples of non-bearing spurs collected June 24 contained 1.87 per cent and 2.88 per cent of starch respectively, figures comparable to those found for Jonathan the year before. Subsequent study of the spur performance on these trees showed that an average of 69 per cent of the spurs on the trees sampled blossomed in 1921.

These findings were substantially confirmed by Harley ('25) who sampled bearing and non-bearing spurs from a Stayman Winesap tree at College Park, Maryland. The procedure followed by Harley both in sampling and in analysis was a distinct improvement over that used in previous work. The samples collected June 27, 1923, and July 9, 1924, comprised spurs of a uniform length that had been found by prior study to be optimal for blossom bud differentiation. The new growth was analysed separately from the one-year-old wood. On both dates the non-bearing spurs contained in the new growth alone 4 per cent or more of starch and the bearing spurs contained similarly 1 per cent or less.

The earliest differentiation of blossom buds on apple trees observed by Kirby ('18) in Iowa was July 1, and the first indication observed by Drinkard ('09–'10) in Virginia was June 20. Both investigators agree that the majority of buds that form blossoms are not differentiated until later. The evidence is therefore fairly conclusive that starch accumulation in the spur immediately prior to the period of bud differentiation is in some way associated with blossom bud formation.

Only one exception to the rule has been reported. This exception was found at New Hampshire in a study of the carbohydrate and nitrogen content of spurs from two plots of Baldwins growing in sod (Kraybill et al '25). One plot had received nitrate of soda and the other had not. The sample from each plot that included the higher percentage of spurs forming blossom buds was lower in nitrogen and higher in starch and other carbohydrates during the period of bud differentiation. However, the sample from the unfertilized plot where 10.4 per cent of the spurs formed blossom buds contained more starch than the sample from the nitrated plot where 42.4 per cent of the spurs formed blossom buds.

An association between carbohydrate accumulation and blossom bud formation evidently does not obtain in this case. The comparison is here between trees growing under different cultural conditions, and since the difference concerns the nitrogen supply, the nitrogen analyses might be expected to throw some light on the situation. The spurs from the unfertilized plot contained less than half of one per cent of nitrogen, the lowest percentage of nitrogen ever found in apple spurs. This in itself suggests that these trees were in an extreme condition, one approaching that described in the classification of Kraus and Kraybill ('18) as feebly vegetative and non-fruitful, nitrogen being low and carbohydrates very

high. The nitrogen supply may be said to be so low that it constituted a limiting factor suppressing both vegetative and reproductive development.

A complete statement of the facts must take into consideration cases of which this instance is in all probability representative. Blossom bud formation on apple spurs has never been found to take place unless there has been a considerable accumulation of starch in the spur, particularly in the new growth, prior to the period of bud differentiation. However, starch accumulation in the spur is not always followed by blossom bud formation. In case the nitrogen content is very low, blossom buds are not formed even though carbohydrates accumulate in the form of starch. It would seem safe to predict that in the absence of any marked accumulation of starch in an apple spur before the period of differentiation, no blossom bud will be formed, and that if starch does accumulate, a blossom bud will develop provided no extreme condition prevails that might inhibit development.

Is this association of blossom bud formation and carbohydrate accumulation purely accidental or does it have some physiological signifiance? Is one phenomenon cause and the other effect or are both common products of the same set of factors? It has been suggested that the absence of starch in bearing spurs is merely an effect of the presence of developing fruit (Potter and Kraybill '25). This is unquestionably correct, but the lack of starch accumulation in the vicinity of the differentiating bud is not thereby prevented being indicative of the course of bud development. The absence of stored starch in the barren spurs of Nixonite and Ben Davis trees shows that blossom buds failed to develop where factors other than the presence of fruit on the spur prevented the accumulation of carbohydrate. The nature of the factors that prevent or determine carbohydrate accumulation in the spur, though interesting from both a theoretical and a practical point of view, has no necessary connection with the nature of the relationship between starch accumulation and blossom bud formation.

It would seem to be out of the question that such an inert material as starch could influence in any decisive manner the morphological development of the growing point, particularly in view of the distance it is removed from the region of starch storage. It is quite conceivable, however, that the accumulation of starch may be merely an easily determined index of a general condition of carbohydrate accumulation and that some more plastic form of carbohydrate may be responsible for a direct effect on the growing point.

What possible connection could there be between carbohydrate accumulation and bud differentiation? Reference to the carbohydrate-nitrogen ratio is after all merely another way of stating the question. By considering other phenomena associated with carbohydrate accumulation it may be possible to find some general tendency, some guiding principle that will throw light on the specific relation to blossom bud formation.

Biennially bearing apple trees in the off year usually present a striking instance of carbohydrate accumulation. This has been shown by actual chemical analyses of both spurs and bark in the case of the York variety (Hooker '20). During a study of York trees that has extended over a period of six years characteristic

differences have been repeatedly observed between bearing and non-bearing trees growing side by side in the same orchard (Hooker '25). Just before the crop is ready to be harvested the trees contain approximately their maximum stores of carbohydrate. At this time the bearing trees have been distinguished by darker foliage which permits their identification from a considerable distance. The non-bearing trees have had smaller, yellower leaves that began to fall in considerable numbers some time before the leaves on the bearing trees. Measurements showed that the spurs have grown more on the trees that are not bearing a crop. This is particularly striking as it is more usual to find greater spur growth the year no fruit is borne. However, the same condition has been observed by other investigators (Crow '20) under similar circumstances.

All of the phenomena associated with the excessive accumulation of carbohydrate in biennially bearing trees during their off year can be produced experimentally. Both Harvey ('23) and Kraybill ('23) have shown by chemical analyses that girdling increases the percentage of carbohydrates above the ring. Shoots and spurs girdled a short time after blossoming will lose their leaves sooner than ungirdled shoots and spurs, as has been shown by some unpublished data obtained by Murneek in Oregon. If a spur bearing an apple or if a bearing branch be girdled, the leaves remain attached to the spur or branch sometime after those on the girdled spur or shoot that is bearing no fruit. Haller and Magness ('25) report the same phenomenon observed under somewhat different conditions. Spurs or branches bearing fruit were girdled and the fruit above the ring was thinned to one apple and a definite number of leaves so as to obtain a range of from 0 to 20 leaves per fruit. Some of the leaves on the ringed branches turned yellow and dropped off during the summer. A count of the remaining leaves made on August 8–10 showed that the greatest dropping was from the branches having a high number of leaves per fruit and that the percentage of leaf fall increased with the number of leaves per fruit. Analyses were not made, but it is reasonable to assume that the carbohydrate accumulation above the ring was likewise proportional to the number of leaves per fruit.

In addition to the effect on leaf fall, girdling has the general tendency to reduce terminal growth, size, and color of leaves and total area of leaf surface. These effects are well known, having been reported by Alderman and Auchter ('16) and a number of other investigators. All the differences observed between the bearing and non-bearing York trees can evidently be produced by girdling. In the one case carbohydrate accumulates in relatively large amounts because of the bearing habit of the variety, in the other case the accumulation of carbohydrate is artificially induced by treatment.

The retardation of growth that appears to be associated with excessive carbohydrate accumulation suggests the possibility of a relation between carbohydrate accumulation and the period of inhibited length growth known as the rest period. After an extensive investigation of the rest period, Howard ('15) came to the conclusion that "rest sets in on account of the inhibition of enzyme activity due to over-accumulation of the products of their work." He referred particularly (compare p. 53) to carbohydrate accumulation reporting that with "a

greatly increased deposition or accumulation of carbohydrates, enzyme activity is soon checked if not almost entirely inhibited." Subsequent investigations at the Missouri Experiment Station (Abbott '23) have shown that in young apple and peach trees carbohydrates do accumulate as the rest period develops and that treatments such as pruning or fertilizer applications that defer carbohydrate accumulation likewise defer the beginning of the rest period. Howard showed that treatment with rest-breaking agents increased the production of carbon dioxide and that the increased production was proportional to the acceleration in growth produced by the rest-breaking agent. Hodgson ('23) observed that starch disappeared from pear, peach, and cherry buds in direct proportion to the duration of etherization, both when the buds were kept warm enough to grow and when growth was inhibited in a cold room. Many analyses might be cited to show the gradual reduction in total available carbohydrates during the winter when the plant is emerging from the state of rest.

The relations between the rest period and carbohydrate may be summarized as follows:

1. The rest period develops gradually and at the same time carbohydrates accumulate.

2. If the accumulation of carbohydrates is deferred, the beginning of the rest period is deferred.

3. The period of middle or most profound rest is coincident with the period of maximum carbohydrate content.

4. The rest period ends gradually over a period during which the carbohydrate content is decreasing.

5. Treatments that hasten the end of the rest period stimulate the consumption of carbohydrate by respiration.

The correlation between the carbohydrate content and the rest period is remarkable and if it be merely a coincidence it is surely a most extraordinary one.

Carbohydrate accumulation seems then to be associated under certain conditions with a paler, more yellowish-green color of the foliage, with smaller leaves, with earlier leaf fall, with retardation of shoot and spur growth, with inhibition of length growth in the tops during the rest period and with the differentiation of blossom buds in the place of leaf buds. What is the collective significance of these facts? Every one of the conditions or processes that is associated with carbohydrate accumulation is also related to carbohydrate production. The growth of shoots which appears to be retarded or inhibited when carbohydrates accumulate, the pigmentation, size and persistence of leaves, the formation of either leaf buds or flowers buds—all these are factors in the development or functioning of the photosynthetic machinery of the plant. The accumulation of carbohydrate would seem to retard or inhibit all processes leading to its production.

The absence of any evidence for a rest period in roots (Curtis '18) and the favorable influence of accumulated carbohydrates on root development in general (Starring '23) constitute negative evidence that supports this thesis. Roots are

carbohydrate consuming, not carbohydrate-producing organs and their growth and development is favored by carbohydrate accumulation.
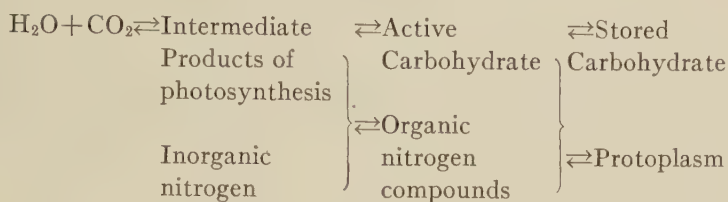
The hypothesis that carbohydrate accumulation tends to retard or inhibit all processes that lead to its production is a special instance of a more general law "that a system tends to change so as to minimize an external disturbance." The biological cogency of this principle was first emphasized by Bancroft ('11) in his Presidential Address before the American Chemical Society in 1910. This theorem appears in a number of forms under a variety of names in different branches of science. It is essentially a corollary of the Second Law of Thermodynamics. To the chemist it is known as LeChatelier's Theorem: "If a system in equilibrium is subjected to a constraint by which the equilibrium is shifted, a reaction takes place which opposes the constraint, that is, one by which its effect is partially annulled. In all cases, whenever changes in the external condition of a system in equilibrium are produced, processes also occur within the system which tend to counteract the effect of the external changes" (Findlay '04). In the case under consideration the external conditions are those that bring about carbohydate assimilation. The resulting accumulation of carbohydrate produces changes within the system that tend to retard or inhibit its production.

Since the hypothseis derived from observed facts and experimental data agrees so well with established principles, there would seem to be some justification for giving it serious consideration. Such being the case, the relation between carbohydrate accumulation and the concomitant retardation of shoot and leaf growth, the rest period, and leaf abscission would appear to be something more than an accidental association. The accumulated carbohydrate becomes a determining factor. It is not, of course, the only factor that might bring about these effects. A retardation of spur growth, for example, occurs in bearing and barren spurs in the absence of any accumulation of carbohydrate. Similarly, carbohydrate accumulation is not to be considered the only factor determining blossom bud formation, though in the apple it would seem to be of major importance. From this point of view the formation of a blossom bud is essentially a morphological response involving the metamorphosis of potential photosynthetic machinery into floral parts.

If it be granted that, in general, carbohydrate accumulation tends to retard all processes leading to its formation and may play a dominant role in determining blossom bud formation, what is the mechanism or organization involved both in the accumulation of carbohydrate and in the retardation of the processes leading to its production?

The accumulation of carbohydrate implies an excess of manufacture over consumption and depends on the relative rates of these two processes. The dominant factor in carbohydrate consumption would seem to be its utilization in growth during the growing season and its respiration during the dormant season. Utilization in growth is the more important for the present discussion. Here nitrogen plays a conspicuous role which is evinced by the inverse relation usually existing between the supply of available nitrogen and the amount of carbohydrate that accumulates. Some of the known carbohydrate-nitrogen relations involved,
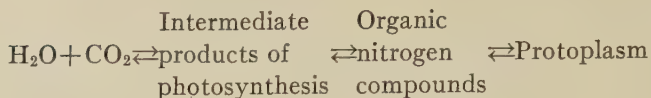
more particularly in shoot growth, may be represented diagrammatically in the following scheme:

$$H_2O + CO_2 \rightleftarrows \text{Intermediate} \quad \rightleftarrows \text{Active} \quad \rightleftarrows \text{Stored}$$

Products of Carbohydrate Carbohydrate
photosynthesis
$$\rightleftarrows \text{Organic}$$
Inorganic nitrogen $\rightleftarrows$ Protoplasm
nitrogen compounds

The diagram indicates what may be accepted as the chief relations obtaining between carbohydrates and nitrogenous compounds. It is apparent that an increase in the supply of nitrogen, whether organic or inorganic, would divert a greater amount of carbohydrate to growth and the synthesis of protoplasm. In consequence the amount of carbohydrate that might be stored would be reduced. Conversely, a decrease in the supply of nitrogen would favor carbohydrate accumulation. A dearth of available nitrogen would inhibit development altogether. Carbohydrate would accumulate but even blossom bud formation might be suppressed as in the case already mentioned of the Baldwin apple trees growing in sod. The absence of available carbohydrate would have a similar limiting action, even in the presence of an abundance of available nitrogen. These are well known facts, amply illustrated in the literature on carbohydrate-nitrogen relations (Hooker '24).

It may be assumed that carbohydrate and organic nitrogen combine in some definite proportion for the synthesis of protoplasm. Here then is a real carbohydrate-nitrogen ratio. It would be of considerable interest to know whether there are different ratios for different tissues and for different organs and to what extent the ratio varies in different plants. In any specific case, as in the shoot growth of apple trees, some more or less constant relation might be expected between the rates at which active carbohydrate and organic nitrogen are produced. Unless they are produced in the exact ratio in which they are used for growth, there must be an accumulation of one or the other. In the apple it would appear that the carbohydrate is produced more rapidly than it is used, because even in young trees not yet of bearing age carbohydrate accumulates before the season is over. It may be doubted whether this holds for all plants. There are indications that in the tomato under the usual conditions of its culture there is no marked accumulation of carbohydrate until the fruit begins to develop. According to Murneek ('26) the fruit makes such a demand for nitrogen on the rest of the plant that growth is retarded and carbohydrates accumulate subsequently. This being true, it constitutes a point of fundamental difference between tomatoes and apples, and suggests that some circumspection be used in applying results obtained with one type of plant to the other.

The formation of organic nitrogen compounds being relatively the slower process in apple trees, it must act as a limiting factor determining the rate of growth. Assuming an unlimited supply of inorganic nitrogen, growth is determined by a series of reactions that includes the organic nitrogen:

$$H_2O + CO_2 \rightleftarrows \begin{array}{c}\text{Intermediate} \\ \text{products of} \\ \text{photosynthesis}\end{array} \rightleftarrows \begin{array}{c}\text{Organic} \\ \text{nitrogen} \\ \text{compounds}\end{array} \rightleftarrows \text{Protoplasm}$$

The determination of growth in the apple by a series of reactions involving nitrogen, even though the supply of inorganic nitrogen does not constitute a limiting factor of growth, throws light on the intimate relation that has been found to exist between the distribution of nitrogen and the relative vigor of growth. Analyses of apple shoots have shown that growth closely parallels the distribution of nitrogen during the period of most active growth (Hooker '24). Terminal shoots which ordinarily make a more vigorous growth than laterals contain the higher percentage of nitrogen at their tips. Nitrate application in the spring increases growth and augments the nitrogen content at the tips of the shoots. The stimulation of growth at the cut ends of headed branches is associated with a local increase in nitrogen. Conversely, the suppression of growth by pruning is associated with the diversion of nitrogen to unpruned laterals or less severely pruned branches.

If growth is determined by a series of reactions it might be expected that the rate of growth would reveal some indication of the consecutive nature of the series of reactions involved. It is revealed as a matter of fact in the shape of the growth curve itself. Growth can be measured by the formula for consecutive reactions derived by Rutherford ('13) to calculate the rate of formation of radioactive substances. A glance at the curve representing the formation of Radium D by a series of consecutive reactions from Radium A shows it to be essentially the same as the typical growth curve. The formula may be written as follows:

$$y = A(1 - ae^{-k_1 t} + be^{-k_2 t} + ce^{-k_3 t} - \ldots \ldots),$$

where y is the amount of growth at time t, A the maximum amount of growth, k_1, k_2, k_3, etc., reaction constants, and a, b, c, constants that can be expressed in terms of the reaction constants as shown by Rutherford. It has been found that any simple growth curve can be expressed by this formula.

It is significant that the formulae that have been proposed for the growth curve are for the most part special cases of this general formula for consecutive reactions. In case the reaction constants k_1, k_2, k_3, etc., can be arranged in an arithmetic series having the ratio $1:2:3$, etc., the formula becomes a binomial that can be written

$$y = A(1 - e^{-k t})^n,$$

where n is the number of consecutive reactions. This is Mitscherlich's formula for growth. If $n = 1$, we have Wilhelmy's formula for growth, that of a simple monomolecular reaction. If the y axis is moved to the point of inflection,

$$y = A(1 - e/n^{-k t})^n.$$

When $n = -1$, this becomes

$$y = A/(1 + e^{-k t})$$

which becomes Robertson's formula for growth when the time is transposed, moving the y axis back.

As indicated in the diagram, some or all of the reactions are reversible. This does not involve any change in the formula. It involves only a change in the meaning of the constants. The maximum amount of growth A, for example, becomes the equilibrium value of y, the value of y at which equilibrium is attained and growth ceases. This is more in agreement with the facts. Growth may be limited by a restricted amount of nutrient material, but it cannot be increased proportionately by any increase in the nutrient supply. The application of fertilizers will not make a currant bush grow as large as a pear tree, though a pear tree may be dwarfed to the size of a currant bush. Under the most favorable nutrient conditions the maximum size of the plant is limited by intrinsic conditions, which we may interpret to be some balance or equilibrium within the plant.

So far the discussion has been confined to the mechanism operative in bringing about an accumulation of carbohydrate. The reactions that have been emphasized as directly involved constitute a mechanism that as far as it goes seems in accord with the known facts. Some of the more obvious implications of the proposed scheme have also been found in accord with the facts. What then is the mechanism or organization involved in the retardation or inhibition of carbohydrate production by its accumulation? If carbohydrate is produced by a series of reversible reactions, it is readily seen that an accumulation of the end products of the consecutive reaction will bring the process to a standstill. The effect of carbohydrate accumulation on the plant is not, however, confined to an inhibition of the photosynthetic process itself. The production of additional photosynthetic machinery is likewise inhibited and to some extent at least the already existing machinery is destroyed. Data are not available to permit a detailed account of the processes that bring this about, but some features of the problem may be emphasized.

The several phenomena which are here considered to be responses to an accumulation of carbohydrate are called forth by varying degrees of carbohydrate accumulation. They may be arranged in the same order in which they appear during the usual seasonal development of the plant. The differentiation of blossom buds in the apple appears to be associated with only a moderate accumulation of carbohydrate. With further accumulation the bud passes into a resting period, while the leaves remain green and active. When the maximum accumulation of carbohydrate is reached, the leaves turn yellow and fall. There would seem to be no particular reason why this order should be maintained in all plants. Some may stop growing and enter a rest period before blossom buds are formed.

Nor does it seem essential that the mechanism involved must be the same in all cases. Sampson ('18) has given us some insight into the chemical changes going on in the abscission layer that are directly responsible for leaf abscission. The part played by pectin-like substances in these changes is strongly suggestive of an ultimate connection with carbohydrate accumulation. There is no reason for assuming that pectin-like substances are in any way involved in the retarda-

tion of growth, in the rest period, or in blossom bud formation, though of course they may be, for all we know. Howard ('15) has suggested that the inhibition of enzyme activity may be responsible for the rest period and this may be an important factor though it can hardly be the only one involved. It is possible that carbohydrate combines with organic nitrogen or other building materials essential for growth in different ratios to form now one kind of tissue now another. Various other suggestions might be advanced, but these are problems for further investigation.

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THE OSMOTIC QUANTITIES OF THE PLANT CELL[1]

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I. SURVEY OF THE OSMOTIC QUANTITIES

To gain a general impression of these quantities the results obtained on a cell, chosen from the pith of a stem of *Impatiens Noli tangere*, are given by way of illustration. The condition of the cell as it was in the plant (or, to be more specific, as it was in pure paraffin oil after being excised) was designated "normal" (*n*) (Fig. 1), and had a volume of 14122 (arbitrarily chosen unit). After being
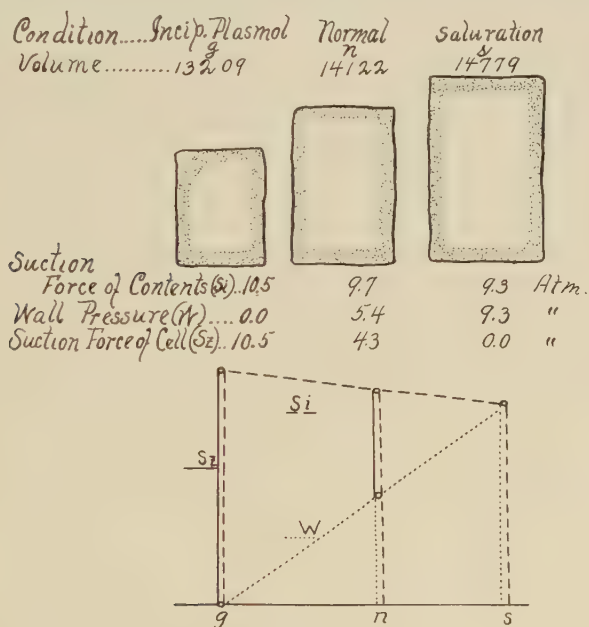
Fig. 1. Osmotic quantities (cell from the pith of *Impatiens*).

immersed in an aqueous solution of cane sugar of sufficient concentration, water was withdrawn from the cell, and its volume was reduced. In the condition of "incipient plasmolysis" (*g*) (Fig. 1) the protoplasm had slightly separated from the wall, which was no longer under tension, and the volume was 13209. Upon being placed in pure water, the cell absorbed some of it, and the volume increased to 14779, which condition was designated as "saturated" (*s*) (Fig. 1).

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The Cell Sap. It was determined by the plasmolytic method that in the condition of incipient plasmolysis the cell sap could suck in water with a force of 10.5 atm. (Fig. 1). It follows that in this condition the cell sap, and the contents of the cell as well, had a suction force of 10.5 atm. ($Si_g = 10.5$ atm.).

Passing from this condition to the normal condition, it is to be noted that the cell sap was more diluted, and its suction force (which was determined from the change in volume) was less, that is, 9.7 atm. ($Si_n = 9.7$ atm.) (Fig. 1). The suction force was proportionately reduced when more water was drawn into the cell, and the saturated condition was attained. It was then 9.3 atm. ($Si_s = 9.3$ atm. (Fig. 1).

The Wall Pressure (*W*). At incipient plasmolysis the wall was not under tension, and hence the pressure was 0 ($Wg = 0.0$ atm.) (Fig. 1). In the saturated condition the maximum pressure prevailed, and no more water could be absorbed, because the wall pressure was equal to the suction force of the contents of the cell ($W_s = Si_s = 9.3$ atm.) (Fig. 1). In the normal condition the wall pressure lay between these two extremes ($W_n = 5.4$ atm.) (Fig. 1). This last value was deduced from the assumption that the increase in pressure is proportional to the increase in volume. The wall pressure (*W*) is defined as the pressure which the wall exerts upon the contents of the cell. Turgor pressure (*T*) is defined as the pressure exerted by the contents of the cell upon the wall. Since action and reaction are equal and opposite in direction, wall pressure and turgor pressure are numerically equal in the isolated cell.

The Suction Force of the Cell. The suction force of the cell is the force with which the entire cell can absorb water. If we regard only the conditions prevailing in the isolated cell, it is the resultant of two antagonistic forces: the suction force of the contents of the cell (*Si*), which tends to draw water into the cell, and the wall pressure which tends to press-water out of the cell. Thus,

Suction Force of Cell = Suction Force of Contents less Wall Pressure, which is symbolized:

$$Sz = Si - W.$$

By means of this formula the following calculations were made for the illustrative cell (Fig. 1):

Suction force of the cell at incipient plasmolysis:

$$Sz_g = Si_g - W_g = 10.5 - 0.0 = 10.5 \text{ atm.}$$

Suction force of the cell in the normal condition:

$$Sz_n = Si_n - W_n = 9.7 - 5.4 = 4.3 \text{ atm.}$$

Suction force of the cell in the saturated condition:

$$Sz_s = Si_s - W_s = 9.3 - 9.3 = 0.0 \text{ atm.}$$

From these considerations it follows:

(1) There are three distinct osmotic quantities: (a) the suction force of the cell; (b) the suction force of the contents of the cell; (c) the wall pressure, that is, turgor pressure.

(2) These quantities bear a definite relation to each other, which is expressed by the suction-force formula.

(3) Each quantity has a different value in the three conditions of the cell (that is, normal, incipient plasmolysis, and saturated).

Graphs of the osmotic quantities were first employed by Höfler. The volume is given along the abscissa and the atmospheres along the ordinate (Fig. 1); Si (— — — —) less W (........) equals Sz(————).

In passing from incipient plasmolysis to saturation, the suction force of the contents drops from 10.5 to 9.3 atm., the wall pressure increases from 0 to 9.3 atm., the suction force of the cell drops from 10.5 to 0 atm. These variations, when unaccompanied by chemical changes within the cell, are greatest in the suction force of the cell, and are almost as great for the wall pressure, but are only slight for the suction force of the contents.

II. SOME HISTORICAL AND CRITICAL REMARKS

Of the nine values of the osmotic quantities illustrated, the suction force of the contents of the cell at incipient plasmolysis was first measured. Pringsheim and Nägeli observed the separation of the plasma from the wall in 1854 and 1855. De Vries introduced the term plasmolysis. In order to determine this value, the cell was placed in a sugar or salt solution of such concentration that the plasma just began to separate from the wall. In the case illustrated (Fig. 1) a cane-sugar solution of 0.38 mol was required. This 0.38 molarity is called the osmotic value at incipient plasmolysis, and is symbolized by Og. The equivalent value in atmospheres, according to the determinations of Morse, is 10.5 atm. It is identical with the suction force of the cell and the suction force of the contents in this condition. For a long time no other value was measured in this domain of research. Regarding the determination of this value, aside from technical imperfections, two errors were commonly made, the one referring to the terminology, the other to the conception of the prevailing conditions. It was correct to call the value 0.38 mol, or its equivalent 10.5 atm. the osmotic value at incipient plasmolysis, or the suction force of the cell in this condition. It was wrong to call it turgor pressure, osmotic pressure, etc. A whole series of terms have been employed as synonymous, although they are different in their force, and in their numerical expression. Regarding the conception of the prevailing conditions, some authors thought the 10.5 atm. represented the actual turgor pressure or the suction force of the cell as it existed normally in the plant.

Illustration I: Suppose an investigator wished to study the water supply. He then tried to determine the suction force of the cell in the normal condition, that is, 4.3 atm. (Fig. 1). He actually found however, 10.5 atm., and often the result was called the turgor pressure. The difference between the value sought and the value found was $10.5 - 4.3 = 6.2$ atm. The error was greater than the value to be determined.

Illustration II: Suppose an investigator wished to study the movements of the guard cells. He evidently tried to determine the turgor pressure which nor-

mally existed in the cell, or 5.4 atm. He actually found 10.5 atm. and made an error of $10.5 - 5.4 = 5.1$ atm. (Fig. 1.).

Later the cryoscopic method was introduced: What quantity did this procedure yield? The sap pressed from the cell evidently has the concentration which existed when the cell had its normal volume. Apart from all technical imperfections, the value determined by this method is the suction force of the contents of the cell in the normal condition. If the sap yielded by an entire organ is employed, as is usually the case, evidently a mean of many values (which may differ widely) is obtained.

If the result obtained by the cryoscopic method be set down as equal to the suction force of the cell in the normal condition, the error made would be 9.7 atm. less 4.3 atm., or 5.4 atm. (Fig. 1).

The literature of the last decades of years is full of such confusions. The chief cause is the faulty terminology. The faulty terminology could hardly have been possible if attention had been paid to the variations in the volume of the cell in the three conditions described. The disregard of these variations is the more astonishing, since the first drawings of De Vries in 1877, which have been reproduced in all text and hand books, clearly indicate the variations in volume.

III. A Survey of the Measurements of Osmotic Quantities

A. Measurements at Incipient Plasmolysis.—These are well known, so that a few remarks will suffice. It is to be emphasized that incipient plasmolysis is an abnormal condition of the cell, but the physiologist is mainly interested in the normal condition. For all that, the plasmolytic method has rendered most valuable service, and one needs but to recall the classic work of de Vries to appreciate this fact. This method will still be very serviceable in the future, provided no impossible demands are made upon it. If for instance, the suction force at incipient plasmolysis of the guard cells of *Convallaria majalis*, standing in the shade of the woods, is found to be 6.7 atm., knowledge of the turgor pressure or of the suction force of the cell in the normal condition may not be claimed. However, when the value obtained is the member of a series of measurements, it may prove to be very instructive; thus it was shown, that after the plants were exposed to the sun, while standing in a water-saturated atmosphere for two hours, the suction force of these cells at incipient plasmolysis increased from 6.7 to 25 atm. Attention was drawn in this way to the fact that great physico-chemical changes which are of interest to the physiologist occur within these cells.

B. Cryoscopic Measurements. Just as for the previous method, the technique will be passed over. Let us emphasize two things:

(1) This method yields a mean value for many hundreds of cells that may have very widely different individual values.

(2) That the suction force of the contents of the cell at the normal volume is found by this method (Fig. 1).

It is clear that if a variation in the results is found, for example if (Si_n) has increased, the increment may be due (a) to the loss of water (the sap becomes more concentrated) or (b) to the formation of an osmotically active solute.

By this method the variations in Si_n may be determined, but not the causes of such variations. A further analysis becomes possible, if the method of incipient plasmolysis be applied, which determines the formation of osmotically active solute. It may be permissible to refer to the fact that the turgor pressure cannot be measured by the cryoscopic method, nor can this method yield the quantity which refers to the influx of water. In the chosen illustration the cryoscopic method yields the value 9.7 atm., the turgor pressure is 5.4 atm., and the quantity referring to the influx of water is 4.3 atm. The suction force of the cell determines the influx of water, and is the resultant of the suction force of the contents of the cell and the wall pressure.

C. Suction-Force Measurements: When the term "Suction Force" alone is here employed, it is understood to mean the suction of the cell at the normal volume. As these measurements have been made almost exclusively in my laboratories the results will be discussed at length.

(1) Up to the present three methods were employed: The first method may be called the "cell method," because the suction force of single cells can be determined by it. It is based on the simple principle that the volume of a cell remains constant in a solution whose suction force is equivalent to the suction force of the cell. In a more concentrated solution, the cell will decrease in volume, and in a less concentrated solution it will increase in volume. In order to measure the suction force of a cell the concentration of the agent is determined in which the volume of the cell does not vary. By means of this method *a survey of the distribution of the suction forces in the plant* was obtained.

Let us consider a given plant. The water, which is taken up by the absorbing cells of the roots, passes from cell to cell in the body of the root, then it enters the conducting strands, passing onward to the stem, leaves, and blossoms along these avenues, and finally supplies every tissue by passing out of the conducting strands, and again from one cell to another. It seems legitimate to make the *a priori* statement that (other things remaining the same) the suction force at a given point is proportional to the resistance encountered by the water which supplies it.

(a) In conformity with this idea, it was attempted to verify an *increment in the osmotic quantities with the increasing height* in a given plant. The quantities formerly determined in the attempt were commonly called "osmotic pressure." In reality, the osmotic value at incipient plasmolysis (Og) (plasmolytic method), or the suction force of the contents in the normal condition (Si_n) (cryoscopic method) were measured.

Let us consider the osmotic value at incipient plasmolysis. The leaves of a beach tree (Table 1) at varying heights were studied. No regular increment in Og could be noted as the height increased. Neither does (Si_n) manifest a regular increment with increasing height, according to the cryoscopic results of *Dixon*; but according to those of Harris, Gortner, and Lawrence, it does (Table 1). The relations sought became apparent at once, when the suction force of the cells at normal volume was determined (Table 1). This is not surprising, since the influx of water is determined by the suction force of the cell, and therefore it is

TABLE 1. INCREMENT IN THE OSMOTIC QUANTITIES WITH INCREASING HEIGHT

Leaves of Fagus, height in m.	Og Mol KNO$_3$				Sz$_n$ Atm.	
	Lower Epid.	Upper Epid.	Lower Epid.	Upper Epid.	Lower Epid.	Upper Epid.
13.0	....	....	....	....	9.9	10.5
11.1	....	....	....	....	9.3	9.9
8.7	....	....	....	....	8.4	9.3
7.0	0.31	0.30				
5.0 (5.5)	0.39	0.39	0.41	0.44		
4.0	....	....	0.41	0.44		
2.7 (2.0)	....	....	0.43	0.47	5.9	7.5
1.0	0.29	0.30	0.45	0.44		
0.5	0.30	0.29				

Leaves, height in ft.	Si$_n$ Atm.		
	Magnolia	Ulmus	Betula
66	....	....	15.6
52	....	....	16.0
38 (30)	19.6	16.5	15.1
25	....	....	14.1
18		10.7	
10 (11)	....	12.4	12.6
4	22.3	13.7	
1	....	9.2	
	Dixon		Harris

this quantity which must be measured. Studies on the Ivy further illustrated the principle (Table 2). The suction force increases in all of the tissues from below upward. No increment was noted in (Og) in this sense, in studies on the stem of *Urtica* (Table 2).

TABLE 2. DISTRIBUTION OF THE SUCTION FORCE OF Og IN THE CROSS-SECTION OF AN ORGAN

		Pith	Hadrome	Inner cortex	Outer cortex	Phellogen	Epidermis
Hedera Sz$_n$ Atm.	Stem at 225 cm.	4.8	4.2	5.0	7.3	—	7.4
	Stem at 35 cm.	2.4	2.1	2.9	3.4	3.7	—
	Root at 5 cm.	—	2.1	2.4	—	3.2	—
	Root at 22 cm. (absorbing zone)	—	—	1.6	—	—	1.0
Urtica Og Mol KNO$_3$	Stem, top	0.35	0.47	0.38	0.44	—	0.39
	Stem, middle	0.40	0.62	0.52	0.55	—	0.43
	Stem, base	0.43	0.66	0.53	0.53	—	0.59

(b) Let us consider the distribution of the suction forces in the cross-section of an organ. According to our best information, the organ obtains its supply of water from the hadrome. In conformity with this view, the minimum suction force was found in the immediate neighborhood of the hadrome, and the values

increased as the distance of the cells from this region became greater (Table 2). An exception to this rule was found in the absorption zone of the root. Here the conditions were reversed, since the water is conducted from the epidermis to the hadrome. The Og relations are quite different. No increment of Og, from a minimum in the region of the hadrome, toward the epidermis could be determined (Table 2).

(c) Consider the variation of the *suction force in the palisade cells* of the ivy leaf. In a row of these cells, passing from one of the principal veins to another, the highest suction force was found midway between the extremities. When the series ran from a principal vein to the border, the maximum was found near the edge. This distribution of the suction forces indicates that, in the main, these cells draw their supply of water from the large veins. In a row of palisades, running from a principal vein into a space where least veins would be encountered, it was noted that the suction force increased regularly from a low value to the remarkably high value of 32.6 atm. (in the 210th cell, Table 3) and then dropped,

TABLE 3. DISTRIBUTION OF THE SUCTION FORCE IN A ROW OF PALISADES CELLS OF THE DRY LEAF (THE FIRST LINE OF FIGURES DENOTES THE CELL NUMBERS, THE SECOND LINE GIVES THE CORRESPONDING SUCTION FORCE IN ATMOSPHERES.)

3	11	21	30	44	60	72	84	99	113	132	145	155	167	190	207	210	214	223	230
12.1	13.3	13.7	15.0	17.1	18.1	20.4	22.7	25.1	26.0	28.4	29.7	30.2	30.7	31.6	31.1	32.6	32.6	32.1	32.1

because another principal vein was being approached. There is no corresponding distribution of the Si_n value in this tissue (Table 4).

When the suction forces in the palisades were studied more closely and the graph of variation was drawn, small local depressions in the regular increment were noted at certain points (see Table 4). At first it was not clear why these

TABLE 4. DISTRIBUTION OF Sz_g IN A ROW OF PALISADES CELLS OF THE IVY LEAF

Cell No.	1	2	3	4	8	9	10	13	14	17	18	20	21	22	23	26	27	28	34	35
Sz_n	10.5	9.9	9.9	11.6	12.1	11.7	12.7	12.4	13.0	13.7	13.3	14.3	14.8	14.3	15.0	15.3	15.0	15.3	15.6	16.4
Sz_g	27	26	27	26	25	26	24	26	26	24	25	27	27	27	27	24	27	25	24	27
Small Vein (×)						×		×			×			×			×			

should appear, but upon checking and examining the anatomy of the subject matter closely, it was found that a local depression corresponded to the proximity of a small vein. Evidently a distinction must be made between the main supply of water drawn laterally from the principal vein and the accessory supply coming from the small veins below.

(d) The distribution of the suction force in the *cross-section of the ivy leaf* is very interesting. Let us restrict our remarks to the palisade cells, the spongy parenchyma, and the epidermal tissues. As was to be expected, the suction force increased in the palisade from the hadrome, that is, from the lowermost layer to the uppermost (see Table 5). In the spongy parenchyma it increased from the

TABLE 5. DISTRIBUTION OF THE SUCTION FORCE IN THE SROSS-SECTION OF THE IVY LEAF

Upper epidermis...............................	8.0 atm.
Palisade.......................................	12.5 12.2 11.9
Hadrome.......................................	—
Spongy parenchyma..	9.8 10.1 10.5 10.8
Lower epidermis...............................	7.3

uppermost region to the lowermost. In conformity with this gradient it might have been expected that the epidermal tissues would manifest the highest suction force, but it actually dropped from 12.5 to 8 atmospheres in the upper epidermis, and from 10.8 to 7.3 atmospheres in the lower epidermis (Table 5). The exceptional position which the epidermal tissues occupy in the series can be understood only if it is assumed that these cells obtain their supply of water laterally from the principal veins, and function as reservoirs of water.

(e) The distribution of the suction force in the *cross-section of the absorption zone of the root* is even more remarkable. The water must run from the absorbing epidermal tissue into the vessels. Accordingly it was found in the root of *Vicia Faba* that the suction force increased gradually from the epidermis to the innermost layer of the cortex cells (Table 6). No further increment could be noted in

TABLE 6. DISTRIBUTION OF THE SUCTION FORCE IN THE ABSORPTION ZONE
OF THE ROOT OF VICIA FABA

Epidermis.................................	0.7 atm.
1. Cortical layer.............................	1.4 atm.
3. Cortical layer.............................	1.5 atm.
4. Cortical layer.............................	2.1 atm.
5. Cortical layer.............................	2.8 atm.
6. Cortical layer.............................	3.0 atm.
Endodermis	1.7 atm.
Pericycle..................................	0.8 atm.
Vascular parenchyma.......................	0.9 atm.

the tissues that lay still deeper within; on the contrary, the endodermis showed the so-called "endodermis jump," that is, the suction force dropped suddenly from 3.0 to 1.7 atm. Some tissues within the central cynlinder manifested a further decrement. Although the endodermis has a lower suction force than the neighboring cortex cells, it must evidently obtain water from them. How is this possible?

(2) Let us pass over the theoretical considerations and confine ourselves to the facts established experimantally, The experiments demanded a new method which made it possible to determine differences in the suction forces of one and the same cell. It was called the *"method for measuring the polar differentiation of the suction forces."* Time will not permit giving an account of the technique of this method. It will suffice to state that this method is closely related to the "cell method," and that it enables one to measure the suction forces separately on the inner and outer side of the endodermis, and the parenchymatous cells of the hadrome. The results are given in table 7. It shows that there is a polar differ-

entiation of the suction forces of the cells studied. The values obtained by the previous method are mean values of the suction forces existing in the cell. By virtue of the polar differentiation of the suction forces, the endodermis can draw water from the cortex cells, and the pericycle can draw water from the endodermis and the vascular parenchyma can take it from the pericycle.—On the inner side of the vascular parenchyma a *negative suction force* was found by means of a special method. From this it follows that the water must be pressed into the vessels. Thus a conception is obtained of the mechanics of bleeding. The interesting facts have thus been revealed that the *endodermis operates like a suction pump and reduction valve*, and that the *parenchyma of the bleeding root operates like a force pump*.

TABLE 7. POLAR DIFFERENTIATION OF THE SUCTION FORCE IN THE ABSORPTION ZONE OF THE ROOT OF VICIA FABA

5. Cortical layer		+3.2 atm.
6. Cortical layer		+4.0 atm.
Endodermis	out	+4.7 atm.
	in	+0.5 atm.
Pericycle		+1.6 atm.
Vascular parenchyma	out	+4.5 atm.
	in	−0.7 atm.
Vessel.		

(3) All of the methods described up to this point have had reference to *individual cells*. They have the merit that they permit the analysis of the suction force distribution in a plant from one cell to another, but the laborious procedure cannot be carried out in every place. A *"simplified method"* has been devised, which offers distinct advantages. Only mean values for a tissue or organ, composed of hundreds of cells, are obtained by it; it has this merit, however, that the operation is simple and *rapid*, and can be carried out in the field. With the aid of this method it becomes possible to measure the following:

(a) The *periodic variations of the suction force* in response to the influence of *exterior factors*. It was found that the factor of the *moisture of the soil* exercises the greatest influence. This factor is not determined so much by the absolute amount of water contained in the soil, as by the force which a plant must exert to draw the water from the soil. The influence can readily be seen from the results given in table 8, which were obtained from the leaf and the petal of two plants growing in the Fribourg Alps. The suction forces were studied in the habitats where the plants grew. The first measurements were made on July 30 and 31, 1923, after an extended drought, and the succeeding measurements were made on the 1st of Aug. after a heavy rain during the previous night. One heavy rainfall sufficed to reduce the suction force in the lamina of *Satureia alpina* from 34.5 to 13.5 atm., that is, 21 atmospheres. The results in the table show also that different species in the same location, even different organs of the same plant (leaf, petal) can show very different reactions.

TABLE 8. INFLUENCE OF THE SOIL MOISTURE ON THE SUCTION FORCE

		Time	Rain	Sz_n	Δ
Satureia alpina Lamina	{	July 30, 11:00 A.M.	before rain	34.5	} 21.0
	{	Aug. 1, 11:00 A.M.	after rain	13.5	
Corolla	{	July 30, 11:00 A.M.	before rain	12.0	} 4.0
	{	Aug. 1, 11:00 A.M.	after rain	8.0	
Biscutella levigata Lamina	{	July 31, 11:00 A.M.	before rain	25.5	} 4.0
	{	Aug. 1, 4:00 P.M.	after rain	21.5	
Corolla	{	July 31, 11:00 A.M.	before rain	14.5	} 0.0
	{	Aug. 1, 4:00 P.M.	after rain	14.5	

The *relative humidity of the air* is the factor which is next in importance. Its influence can be seen from the graph of the *diurnal variation* of the suction force in the ligular florets of *Bellis* on July 26, 1923. The suction force rises from about 7.5 atm. at 6:00 A.M. to about 14 atm. at 2:00 P.M., and falls during noon and night to about 6 atm. at 5:00 A.M. on the following morning. A study of the exterior factors showed that this variation was caused mainly by the variation of the relative humidity, the curve of which is almost symmetrical with the suction-force curve (Fig. 2).
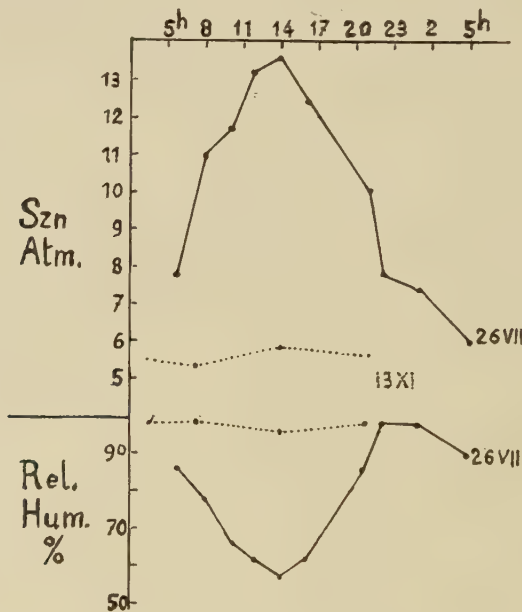
Fig. 2. Diurnal variation of the suction force in the ligular florets of *Bellis*

On the 13th of Nov. when the relative humidity varied only slightly, the variation of the suction force was slight (Fig. 2).

Figure 3 shows clearly the *variation in the suction force* of the ligular florets of *Bellis* during July 1923. The recorded values were always determined at 8:00 A.M. No relation to the humidity of the air can be recognized, but there is an evident dependence on the moisture of the soil. In the first half of the month there was very little rain (Fig. 3). The soil dried and the suction force increased accordingly, from 5.4 to 15.6 atm. The drop beginning on the 14th was caused by the rain which began to fall at that time. It is evident that the increasing moisture of the soil causes a steady decrement in the suction force. The rise of the suction-force curve, in the second half of July, corresponds to another period of drought, and the sharp descent on Aug. 1 to a heavy rain. The sub-minimum
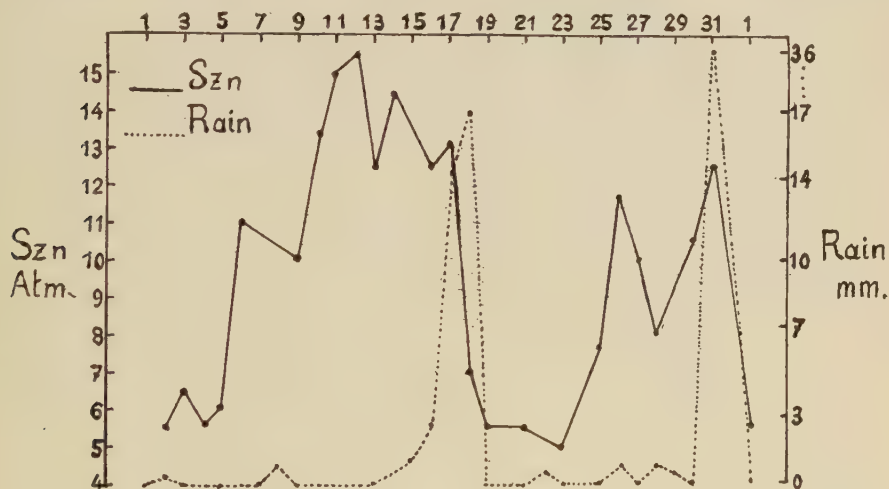
Fig. 3. Variation in the suction force of the ligular florets of *Bellis* during July 1923.

on July 28 corresponds to a preceding precipitation, but the sub-minimum of July 13 could not be explained (rain began to fall only on the 14) until it was learned that the gardener had sprinkled the plants in spite of orders to the contrary.

Even greater deviation is indicated by the curve for the *variations during one year*. A mean value is given for each month. That portion of the Sz_n Sg_n curve which is in full, refers to the corolla, while the interrupted portion refers to the leaf. The precipitation curve is dotted (Fig. 4). In these also a maximum value of the suction force corresponds to a minimum precipitation and the principal minimum of the suction force corresponds to the maximum precipitation (Fig. 4). Some details of the suction-force curve are not clear from the summary mean monthly values of the precipitation. Thus the mean precipitation for July was greater than in June, but the suction force, which accordingly might be expected to drop, actually rises. This behavior clears up when the distribution of the precipitation within each month is taken into consideration. In July, as was seen,

there were two major periods of drought, which caused the suction force to rise, in June the precipitations were more regularly distributed throughout the month, so that the suction force remained low. Apart from these facts, it is evident from *a priori* considerations, that the suction force depends on the *distribution*, as well as on the *quantity* of the precipitation.

(b) With the simplified method it was furthermore possible to study the influence of *habitat* on the suction force, and therefore it is of value in the domain of *plant geography*. In order to obtain useful data it is, however, necessary to take into consideration several sources of error. From what has been said above, it is clear that in the same organ of a plant, remaining in the same location, the suction force can vary from 10 to 20 atm. in a relatively short time. Besides,
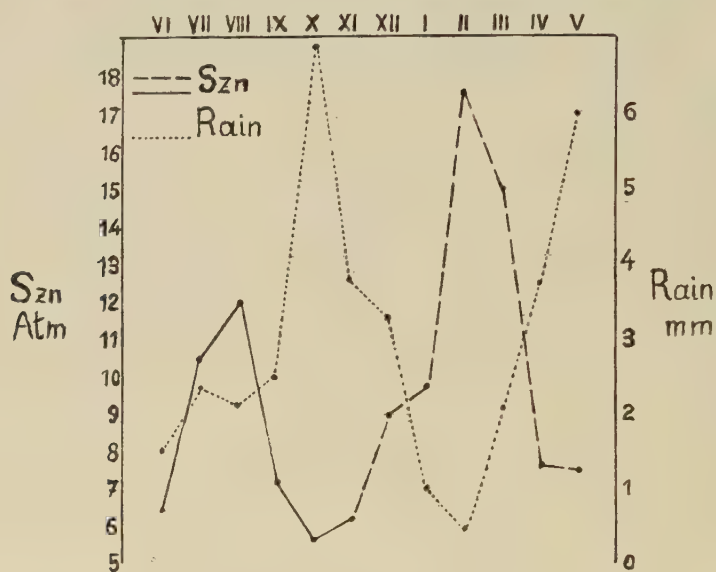
Fig. 4. Variation of the suction force during one year.

different species growing in the same place can simultaneously manifest widely different suction forces, for example, the leaf of *Amelanchier* can manifest 44.5 atm. while that of *Sedum album* shows 8.0 atm. It is best to measure the suction force of the *same species* in different habitats *simultaneously*. Comparable measurements on the vexillum of *Lotus corniculatus*, growing in the Fribourg Alps, are given in table 9. Insofar as the conditions could be judged without

TABLE 9. RELATION BETWEEN SUCTION FORCE AND ALPINE HABITATS
ILLUSTRATED BY THE VEXILLUM OF LOTUS CORNICULATUS

Moist sod	9.5 atm.
Alpine meadow	14.5 atm.
Rock crevice	21.5 atm.
Rock fissure	26.5 atm.
Humus belt	29.5 atm.
Rubble	34.5 atm.

special examination, it appeared that the suction force increases with the dryness of the soil. Measurements made in the plain pointed to the same principle. The differences in the suction forces are evidently due to the difference in the water-balance.

The *comparison* of the *suction forces* obtained in the *plain* and in the *mountains* is particularly interesting. From *a priori* considerations higher values might be expected in the mountains than in the plain, but it is to be remarked that the actual comparison made in the dry summer of 1923 did not manifest a marked difference.

Time does not permit us to enlarge further upon these geographical problems. Let us refer only to the fact that Schimper's hypothesis of physiological dryness of soils could not be verified for peaty substrata.

D. MEASUREMENT OF THE TURGOR PRESSURE

The turgor pressure within a given cell was measured by means of a new method, which cannot be described for the lack of time.

The results found in the study of the relations existing between the *diameter of the stomatal pore and the turgor pressure* of the guard cells, in the leaf of *Con-*

TABLE 10. RELATION BETWEEN THE TURGOR PRESSURE AND THE WIDTH OF THE STOMATAL PORE

Turgor pressure	Width of pore
0— 1 atm.	0.4 atm.
1— 2 atm.	1.0 atm.
2— 3 atm.	1.6 atm.
3— 4 atm.	2.1 atm.
4— 8 atm.	2.6 atm.
8—10 atm.	3.8 atm.
10—17 atm.	7.0 atm.

vallaria majalis, are given in Table 10. The diameter increases with the pressure in harmony with Schwendener's theory.

We will conclude with a few remarks on the *relation* between the *growth of a cell* and the *osmotic quantities*. The relation between growth and turgor pressure was sought in vain for a long time. The cause of the failure was the same as in the failure to establish the suction-force relations, that is, quantities other than the ones actually desired, were measured. Instead of turgor pressure the osmotic value at incipient plasmolysis was determined.

In table 11 the zone of greatest growth is underlined. Og is greatest at the tip and decreases upward along the root. No relation exists between Og and growth. There is a relation between the turgor pressure and growth, but it is different from what it was held to be. The maximum growth does not coincide with *maximum* turgor pressure, as was expected, but with the *minimum* of turgor pressure. On the other hand the suction-force value runs parallel with growth. This is not so surprising since the increase in volume depends chiefly on the influx of water.

TABLE 11.   OSMOTIC QUANTITIES IN THE ROOT-TIP OF VICIA FABA

Tissue examined	Distance from the growing Point in mm.	Og in mol cane sugar	Sz_n in Atm.	T in atm.
Epidermis	1.5	0.50	7.4	3.9
or	3	0.49	7.7	4.0
outer cortex	5	0.47	10.0	2.7
cells	8	0.45	0.4	9.4

In like manner the maximum growth on the convex side of a root, which curves in response to geotropism, coincides with least turgor pressure and max-

TABLE 12.   OSMOTIC QUANTITIES IN THE GEOTROPICALLY CURVING ROOT-TIP OF VICIA FABA

Tissue examined	Side	Og in mol cane sugar	Sz_n in atm.	T in atm.
Outer cortex	concave	0.40	0.5	8.0
cells	convex	0.38	8.2	1.3

imum suction force, while Og is practically the same on the concave and convex side (Table 12).

QUANTITATIVE ASPECTS OF THE PROBLEM OF GROWTH AND DIFFERENTIATION[1]

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One of the most unique properties—if not *the* unique property—of organic beings is their power to grow, to become something which formerly they were not. So far as the ontogenetic process is concerned it appears to be irreversible, the oak cannot be put back into the acorn, except in so far as it may produce acorns, each of which contains the embryo of an oak.

Simplicity is not one of the characteristics of the growth process; on the contrary, many interdependent factors (both known and unknown) participate in it.

In its essence, however, we may regard growth as the transformation of unorganized external material into the organized substance of the plant or animal. It is also evident from a little study that this transformation proceeds in an orderly fashion. Having found that the organism increases in size (or in numbers) in orderly fashion, it is also readily seen that its growth bears some kind of mathematical relation to the time.

QUANTITATIVE ASPECTS OF THE GROWTH RATE

The growth of an organism usually begins at a slow rate, gradually increases for a time, then as the organism approaches maturity it goes more slowly and finally no further increases are perceptible. Many chemical reactions proceed in the same way, especially those in which an autocatalyst is concerned.

The chemist studying the transformations of a pure substance in the laboratory may follow the process much more definitely than one who attempts the same with the more complex growth process. Nevertheless, the application of quantitative methods to the study of this, and other, physiological problems in recent years has greatly advanced our knowledge and makes it more apparent that the growth process is in essence another manifestation of the energy relationships prevailing in other forms of matter.

The mathematical expression of the growth process is to some the most significant, and to others the most trivial, aspect of the problem. Without attempting to argue the question I shall present some of the results obtained from quantitative studies, leaving the hearer to judge of their success or failure.

The Wilhelmy equation used to express monomolecular reactions is useful for some cases especially when the initial lag period of growth is abbreviated.

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[1] Presented before the International Congress of Plant Sciences, Section of Physiology, Ithaca, New York, Aug. 17, 1926.

$$x = A(1 - e^{-kt})$$

$x =$ the size of the organism at time t, $A =$ the final size or limiting value of x, $e =$ the base of the natural logarithms, and $k =$ a constant. The value of k may be found from the equation.

$$k = \frac{1}{t} \log \frac{A}{A - x}.$$

This equation means that the rate of growth at any time is a function of the amount yet to grow, because

$$\frac{dx}{dt} = k(A - x)$$

This equation can only therefore apply roughly because the maximum velocity of growth of most organisms is not in the earliest stages of their development.

Mitscherlich ('19) has expressed the growth of plants by

$$x = A(1 - e^{-kt})^n$$

in which n is the number of environmental factors influencing growth under given conditions. Unfortunately, however, the number of factors and their relation to the growth process cannot now be evaluated. This equation rests upon another theoretical basis, namely, the law of diminishing returns. The increase in yield of a crop due to the addition of nutrients is well known to be greater when the nutrient level is low, and to decrease with each successive addition of nutrients until a point is reached beyond which no further increase in yield results from increasing the supply.

In my own work I have made frequent use of the equation for autocatalysis in the form presented by Robertson. This equation has been used successfully to analyse the growth processes of organisms and admirably serves the purpose of a physiologist. Other equations may be as good, or better, but one must use the tools at hand until better can be found. We may give attention to the equation as commonly used:

$$\log \frac{x}{A - x} = K(t - t_1)$$

in which x is the size of the organism at time t, A is the maximum size attained at maturity, k is a constant, and t_1 is the time at which the organism is half grown, that is, $x = A/2$. Those who are interested in the derivation of this equation may consult Robertson ('23). When values of x are plotted for corresponding values of t, they are found to lie on a sigmoid curve which is symmetrical about the mid-point, that is, where $x = \frac{1}{2}A$. Time may be taken from any point of origin and reckoned in any unit. Changing the value of t_1 shifts the curve bodily to left or right. Changing the value of K changes the general slope of the curve, as K is increased the slope becomes steeper. A study of these parameters allows one to reach conclusions which would be otherwise difficult, or even impossible.

The magnitude of A is probably dependent to a large extent upon nutritional or other conditions constituting the environment of the organism. In practice

we always assume the value of A to be somewhat greater than the observed values. On the contrary, $k(=K/a)$ appears to be representative of something internal in character, the specific velocity constant of the growth process itself. This constant is independent of environmental conditions and expresses the velocity of transformation of unit mass of nutritional materials into tissue substance. Whether the value of k can be specifically related to race or genus remains to be seen. Robertson favors such an assumption, but there are many who find themselves unable to go that far.

I shall give one example which appears to support that assumption. A population of Helianthus plants (Reed and Holland '19) was divided into four groups classified according to their heights at maturity, and the mean value of K determined for each group. Although the mean heights at maturity ranged from 198 cm. in the shortest group, to 312 cm. in the tallest group, there was remarkable constancy in the values of K, in fact, the values were within the range of their probable errors (Table 1). The dispersion of the growth constants from their means, as measured by their standard deviations, shows that the growth rates of the larger deviated more widely than those of the smaller plants.

TABLE 1. HEIGHT AND GROWTH CONSTANTS OF SUNFLOWER PLANTS

Quartile

	I	II	III	[1] IV
Mean final height of plants at maturity	198 cm.	238 cm.	272 cm.	312 cm.
Mean value of K	$0.0440 \pm .0011$	0.0421 ± 0.0016	0.0429 ± 0.0017	0.0443 ± 0.0023
Standard deviation of values of K	$0.0052 \pm .0008$	0.0079 ± 0.0011	0.0079 ± 0.0012	0.0111 ± 0.0016
Values of $\dfrac{A}{K}$	4500	5653	6340	7043

The growth of shoots on apricot trees lends some support to this idea. The weekly elongation and the total length of shoots on trees which had been severely pruned was greater than on trees which had not been pruned the preceding year (Reed '20[a]). Employing the equation: $x = A(1-e^{-kt})$. The equation for growth of the severely pruned is: $x = 230(1-e^{-0.09t})$ for the unpruned it is: $x = 100(1-e^{-0.09t})$ Although I here used Wilhelmy's equation instead of that for autocatalysis, it is an equation of the first order and serves quite well for some types of growth. The inportant thing to be noticed is the identity of the constant in the exponent of e in both equations and the dissimilar values of A, the maximum growth attained.

If the foregoing assumptions concerning the specific velocity constant are correctly taken, there must be something else which determines the final size of the organism. Gaines and Nevens ('25) have made the interesting suggestion that A/K is a specific constant representing final growth capacity whose value as an index of growth capacity or crop yield depends upon the association between the length of time that the crop or one of its constituents continues to grow and

the final extent of growth. This obviously ought to follow, and the authors found evidence for the correctness of the assumption with the plants they studied.

The S-shaped curves (Fig. 1) representing the growth of an organism may be divided into three parts. The lower part (a) represents the initial period in which the size increases rather slowly; the middle portion (b) represents the period of most rapid growth; and the third (c) represents the period commonly known as the period of senescence.

Since the curve plotted from the equation represents the growth of a wide range of organisms, we must guard against giving it too narrow an interpretation.
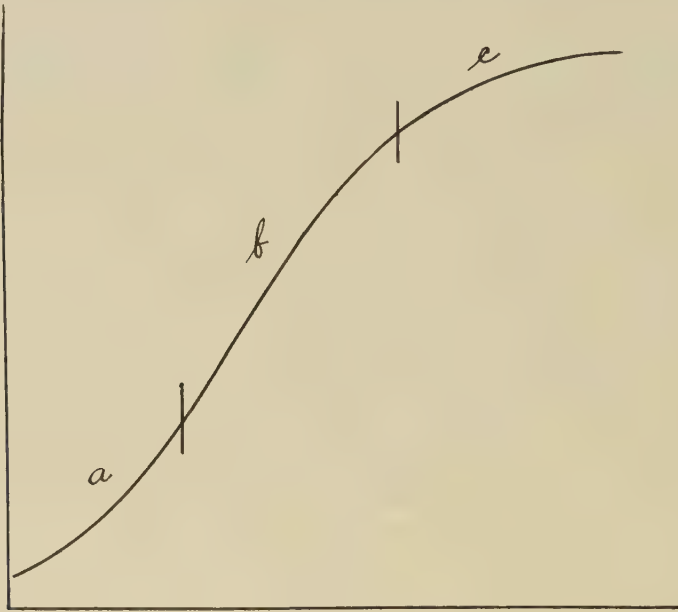
Fig. 1. Typical growth curve drawn from data on the growth of shoots of the pear (*Pyrus*) tree.

The growth represented by (a) undoubtedly is the result of an increase in the number of cells when they increase at a geometrical rate (the growth is an exponential function of time), while the supply of raw material in the environment is greatly in excess of the absorbing capacity of the organism. In the case of yeast and bacteria the number of cells is small in proportion to the volume of the nutrient medium. In the case of the higher plants, the young seedling or young shoot first draws on accumulated products of metabolism of the parent plant, gradually supplementing them with products synthesized in its own tissues. In case of mammals, the young are utilizing during this period the nutrient fluids of the mother, which are especially rich in growth-promoting materials, and are gradually supplementing them with food from other sources.

The portion of the curve represented by (b) covers the period of most rapid growth and is the most conspicuous to the observer. Many physiologists who

have studied growth have confined themselves to this part of the growth process. During this time the increase in size is almost (but not exactly) proportional to the time, that is, the cells increase (in size or number) at an arithmetical rate. We may assume that during this period the catalyst of growth is abundant, but that the growth is conditioned upon the rate at which the organism can obtain from the environment the materials upon which the catalyst can work. During this period growth is more apt to be influenced by fluctuations in the external medium than in the other two periods. In many cases growth during this period must depend upon the rate of oxygen absorption, and in the case of green plants, upon the rate of carbon-dioxide absorption. In all cases it is closely conditioned upon the rate of water absorption, and may therefore depend upon the rate at which acids are produced.

The last portion of the curve covers the period of senescence. The growth during this period comes to a point where no further increase in size takes place; as a matter of fact, some organisms may shrink because of the loss of water. The portion of the curve represented by (c) is symmetrical with (a) in the case of most organisms whose growth curves have been studied. Both portions are obtained when the values of $\pm K(t-t_1)$ approach a maximum. During the period represented by (c) the cells increase in size or number at a rate only slightly greater than that at which cells die. Since the means for obtaining material are well developed, and the supplies of external material are not commonly depleted, we must assume that something has happened to retard the growth of the organism.

One commonly finds that the computed values are larger than the observed during the early life of the plant. Mr. Furusawa has suggested (in an unpublished manuscript) that separate constants for the right hand side of the equation should be obtained. Other workers have usually disregarded this discrepancy. It seems better to try to explain this difference than to avoid it. There is here an opportunity for some experimental work to find whether this lag is due to structural, inherited, or environmental factors.

The use of this equation to represent the rate of growth deserves attention. The differential equation from which Robertson's equation is derived is

$$\frac{dx}{dt} = kx(A-x)$$

a, x, and t represent the same values as before, but $k = K/a$. When values of dx/dt are plotted for corresponding values of x and t, one obtains a bell shaped curve, showing as already intimated that the maximum velocity of growth occurs at the time the plant has reached half its final size. When $x < a/2$ the curve rises and when $x > a/2$ the curve falls. Generally speaking, the correspondence between observed and calculated values of the velocity is good.

Professor Blackman has drawn attention to the advantage of the compound interest law for interpreting the growth of the plants. The original weight of the plant is comparable to the capital, and the growth constant to the rate of interest.

$$W = W_o e^{rt} \text{ or } log\frac{W}{W_o} = rt$$

Blackman ('19) very successfully pointed out the physiological significance of this equation for growth. Determination of the value of r (the efficiency index) is of important in many physiological processes and is comparable to the significance of k in the autocatalytic equation. It is obvious that the value of r does not remain constant through the entire grand period of growth and those who wish to complete the growth curve with a single equation will need to use one of the other forms.

As a mathematical expression of the growth curve the equation used by Pearl and Reed ('22) is undoubtedly more elegant and accurate than any yet mentioned.

$$y = d + \frac{k}{1 + me^{a_1 x + a_2 x_2 + a_3 x_3}}$$

y = size at time x, d = total growth attained in previous cycles, k = final or limiting, size at maturity, a_0, a_1, a_2, and a_3 are constants. This type of curve has given good graphs of the growth of population as well as such problems as the growth of animals and plants.

GROWTH CYCLES

A brief experience with growth curves of organisms will show that cyclic or periodic growth is common. The quantitative treatment of these cycles presents certain problems, but none are necessarily insoluble. These cycles overlap to some extent and it is often impossible to discern their exact limits. Indeed, the more we know about them the less reason we have to expect that they have any well marked boundaries.

In man there are three post-natal cycles of growth: infantile, juvenile and adolescent. The existence of intra-seasonal cycles of growth in the shoots of certain trees has been shown to be quite independent of definite fluctuations in environmental conditions. A more extended inquiry will undoubtedly show many cases of cyclic growth in plants. Laughlin's ('19) quantitative studies on the periodicity of cell divisions in onion root tips point the way to fruitful investigations.

The measurement of a population of shoots on young apricot trees (Reed '20) showed three definite cycles of growth, each conforming to the type of growth curve above discussed.

The first cycle covered the period 0 to 8 weeks, the second from 9 to 17 weeks, and the third from 18 to 28 weeks. The values of A for the three cycles were taken as 110.4, 69.7 and 45.8 cm.

The correspondence of observed and calculated values was satisfactory in each cycle. The values of the growth constant K showed comparatively little variability in the three cycles, but those of K were less constant. The progressive decline in the values of A/K may indicate, as Gaines and Nevens ('25) have suggested, a progressive lowering of the growth capacity of the shoots.

There seems to be little doubt that these fluctuations in the rate of elongation have a real physiological significance. Certain aspects of this problem have already been published (Reed '21) in which I showed that sap concentration and growth seemed to be inversely related. When growth was rapid the concentration (measured by the freezing point depression) was less and *vice versa*. Expressed in the form of a coefficient of correlation I obtained values of *r* approximating —0.600.

TABLE 2. COMPARISON OF THE CONSTANTS OF THE CURVES FOR INTRASEASONAL CYCLES OF GROWTH OF APRICOT SHOOTS

	CYCLE		
	I	II	III
K	0.380	0.355	0.0277
k	0.000344	0.000509	0.000605
$\dfrac{A}{K}$	2895	1964	1653

Attention has been directed to the diminishing growth capacity shown by the values of A/K in table, associated with which I found a gradually increasing concentration of sap in similar shoots. It seems apparent that factors which contribute to the higher sap concentration of the unpruned trees are associated with the growth they made. Their slower growth and consequent diminished draft on the plastic materials of the tree should allow a greater accumulation of soluble materials in their tissues. The smaller water content of the slow-growing wood also contributes to a higher sap concentration.

Reverting to the nature of the growth process in this population of apricot shoots, it seemed worth while to consider another form of growth curve and its mathematical expression. There is a possibility that their length growth followed the course of a reaction which consisted of two consecutive monomolecular reactions, one of which at first accelerated and later retarded the other. The Wilhelmy equation, as above stated, formed the basis of the attempt from which the equation of the curve was worked out.

$$x = 210\left[1 - e^{-0.095\,(t-1)}\right] + 19.1\left[e^{-0.055t}\,cos\,\frac{\pi}{14}t\right]$$

This was considered to show that the main reaction (expressed by the first term) was periodically accelerated and retarded by another term (expressed as a function of *t* involving the cosine). While the assumptions made cannot be pushed too far with the data now available, it does seem apparent that the cycles of growth had a real existence and that they may be studied as *processes* of some sort.

QUANTITATIVE ASPECTS OF DIFFERENTIATION

If quantitative methods have succeeded in permitting us to learn something about the process of growth they should also discover something about that phase of growth which leads to differentiation. The usefulness of the statistical

method for this sort of inquiry has hardly been appreciated by botanists. It has proved that it is possible to learn more about relationships of a group from its statistical than from its individual characteristics. There are attributes which can only be determined by the study of all the group, and in what I have to say about the quantitative aspects of differentiation I shall discuss results which were obtained from a quantitative study of descriptive data.

It is quite apparent that the form of a plant would be quite regular if all the buds on the shoot developed into shoots. Many plants which grow in water have a symmetrical development. But the plants which live in a fluctuating environment are not usually symmetrical except in a restricted fashion. The pattern of the organism is also influenced by the accumulation of metabolic products in certain regions. The rate at which they accumulate and the rate at which they are transformed may therefore play a part in differentiation.

Growth and differentiation lead to a quantitative distribution of matter in space which makes it necessary to regard the position and size of organs as the expression of a definite function. This definite system of differentiation is well exemplified by the size and position of the shoots of the pear tree where the longest lateral is usually produced at the apex (distal end) of the upright mother shoot. The lengths of the other laterals arranged in basipetal order form a descending series. The lengths of the first half dozen laterals descend very rapidly; indeed from that point there is no further decrease in length. In the language of the horticulturist, the first few buds formed shoots and the rest formed fruit spurs. The curve of length of the laterals was expressed by the equation

$$y = 92.47 + 4.193\,x - 136.907\ log\ x$$

where $y =$ length of lateral and $x =$ its ordinal position on the mother shoot.

Pearl ('07) found that the size of a leaf whorl in *Ceratophyllum* increased from the proximal to the distal part of the plant in a way which was well represented by the equation

$$y = a + c\ log\ (x - a)$$

This equation indicates that the size of any particular whorl of leaves is a function (in the mathematical sense) of the number of whorls which have been previously formed on that axis.

The problem of the distribution and the length of apricot shoots on the stem axis was briefly studied by the writer (Reed '24). Casual observation of an apricot branch shows that primary laterals occurred in three fairly well defined groups. The laterals occupying the center of a group were those of maximum length, from which their length gradually decreased. The group of laterals nearest the proximal end of the branch was the largest and produced the longest laterals. The second group consisted of fewer and shorter laterals than the first and was separated from it by an average of 20 nodes which remained dormant. The third group of laterals was not so well defined as the others, but showed many of the same features.

The symmetrical arrangement of the laterals in each group is a feature which suggested that their lengths conformed to a logarithmic curve.

When the scale of mean lateral length for each branch was arranged so that the center of group I fell on node 48 the three symmetrically shaped groups of laterals were easily distinguishable.

If we assume that the cyclic growth of the laterals was in some way similar to the cyclic growth of the branches which bore them, the summations of their length, beginning at the base of the branch, should give a curve resembling that of growth. It was actually found that their values agreed closely with an equation of the general form

$$log \frac{y}{a-y} = K\ (x-x_1)$$

where $y=$ length of lateral grown from node x; $x_1=$ the node at which y had had attained half the length of a for the cycle; $a=$ the maximum, or limiting, value of y; and $K=$ a constant.

If the lengths of the individual laterals be regarded as increments in the length of a system, then the differential form of the above equation ought to express their lengths for each nodal position.

$$z = \frac{dy}{dx} = ky\ (a-y)$$

here

$$k = \frac{K}{a}$$

This was found actually to be the case and the calculated values were in good agreement with the observed. The three curves showed the decreasing amplitude chracteristic of the groups of laterals on the main branch.

The results seem to justify the conclusion that the length of each primary lateral is a function of its position in its group, and consequently, of its position on the branch. The growth processes concerned with the production of laterals on these branches therefore bring about a definite spatial distribution of mass.

In view of the importance of relationships between the size of an organ and its position on the plant for an understanding of the "pattern" or habit of "growth," it is unfortunate that so few attempts have been made to study it.

Within the year Penrose ('25) has called attention to the principles which determine the sizes of repeating structures in the higher plants where each new part possesses growth attributes like those of the apical meristem of the parent shoot. The length of the successive members determines the outline of the organism. Penrose has found that the length (x) of any member is given by the general equation

$$x = A\ (1-e^{-L/A})$$

where L/A is the ratio between, L, the distance of the organ from the base of the stem and, A, the length of the whole stem. The structure of the organism seems to be determined by a type of growth corresponding to that which may be expressed by an algebraic equation of the first degree.

The total output of differential material as measured by the length of lateral branches on a shoot tends toward uniformity (Reed '21a, '24). There is vari-

ability, of course, but no more than one finds in the lengths of the mother shoots themselves. Whether the pear mother shoot produced three or twenty laterals in the first year, their total lengths showed a root-mean-square deviation of less than 10 per cent of the mean. The resulting branch-systems range from a system composed of fewer but longer laterals to one composed of many, but shorter, laterals.

We pass next to consider the length of the laterals on a branch, since this phase of differentiation is one which influences the pattern of the plant. The longest laterals are not necessarily the oldest, nor those at the extremity of the mother shoot.

The branches of fruit trees produce many more short laterals than long. When histograms representing the distribution of length are drawn they show an unsymmetrical distribution about the mean due to the higher frequencies in the lower classes. The distribution of short laterals on many trees determines in large measure their capacity for producing fruit.

The distribution of apricot laterals has a pronounced asymmetry due to the predominance of short laterals, the mean length of 2528 primary laterals having a coefficient of variability of 110.53 ± 1.95. Symmetrical distributions were also found in *Ceratophyllum* (Pearl '07), short branches being produced with much greater frequency than long branches.

These facts taken together are good evidence that the length of shoots on a tree or plant is governed by some very definite factor so fixed in its action that the law of chance is practically eliminated.

The number of blossoms per branch has been but little studied with respect to distribution, yet it is an important phase of differentiation. The blossom is a highly energized center on the vegetative organs toward which some of the most important synthetic materials migrate from other parts of the tree. One may assume that substances moving into the branch go either to the formation of laterals or to the formation of flower rudiments, but the coefficient of correlation speaks against the validity of such an assumption.

$$r = 0.386 \pm .065$$

The coefficient is positive and indicates that factors which increase the number of laterals also increase the number of flower buds. It is not improbable that the formation of primary laterals, through their power to increase the quantity of photosynthates, increases the formation of flower buds. The interdependent processes have a unity which impels them to work together, and not antagonistically in differentiation.

Another step in the study of the problem consists in attempting to learn what relation there is between the length of a lateral and the number of blossoms it can produce. There is an opinion current that short laterals bear a proportionally larger number of blossoms, but the impression may be due to the fact that the blossoms on them must of necessity be closer together and hence more conspicuous.

I determined the following coefficients of correlation. If

$$a' = \text{number of blossoms on primary laterals,}$$
$$b' = \text{number of nodes on primary laterals,}$$
$$c' = \text{length of primary laterals,}$$

the coefficients of gross correlation are

$$r_{a'b'} = 0.099 \pm 0.020$$
$$r_{a'c'} = 0.077 \pm 0.020,$$
$$r_{b'c'} = 0.969 \pm 0.014,$$

and the coefficient of partial correlation is

$$r_{a'b''.c''} = .059 \pm .021$$

This coefficient shows plainly that there is no correlation between the number of blossoms and the number of nodes on a lateral.
Similarly for secondary laterals

$$r_{a''b''.c''} = -0.002 \pm 0.018$$

Here there is no correlation between the numbers of blossoms and nodes upon the secondary laterals.

The relation between the position of a lateral and the number of blossoms it bore was also investigated, in order to see whether the lower (proximal) laterals produced more or less blossoms than the upper (distal) laterals on the branch. The coefficient of correlation in this case was

$$r = -.109 \pm 0.022$$

This small degree of negative correlation may be interpreted to mean that the lower laterals were only slightly, if at all, superior to the others in the production of blossoms.

These results indicate that the laterals of the apricot tree tend toward remarkable uniformity in the production of blossom buds.

Concluding Discussion

The process of growth is influenced by many interdependent factors, yet the organism has an ability to coordinate a multiplicity into unity. When the results of all the processes are integrated we have the organism as the final product. The application of a few simple mathematical principles gives a basis for a rational interpretation of growth. The essentials of the process appear to be concerned with a slow transformation of materials at a proportional to time, resembling transformations which are known in other systems.

The length of a lateral is some sort of a function of its ordinal position on the branch which bore it. The ordinal position also involves the time-relation. This is not to imply that the equation giving the length of the lateral will necessarily explain the causes of its growth, but it does express concisely the sort of organic relationship which exists between the different parts of the tree. Before one can

understand the laws of development it seems necessary to know something about these relationships. With the results at hand it seems logical to regard the problem of differentiation as a process which leads to a definite distribution of matter in space.

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ENVIRONMENTAL COMPLEXES CONSIDERED AS DYNAMIC SYSTEMS[1]

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The organism and its environment may be regarded as the two portions, internal and external, of a single system of material and energy. This enormous system really includes the entire universe and is consequently practically without limits. In studying the changes or processes that go on in an organism it is necessary to consider these two portions separately, and physiology and ecology give special attention to the interactions that occur between them. Although we commonly deal with the organism and its surroundings in this way, as distinct systems, we realize that both matter and energy are continually and restlessly migrating from one to the other, in both directions. For many processes the distinction between the two systems is easy on a common-sense basis (as the change of starch and water to sugar within a cell), but in many other cases it is not so easy (as the vaporization of water from cell walls into a sub-stomatal cavity). Perhaps the most generally satisfactory criterion for distinguishing organism from environment is based on spatial limits; we may say that all changes are internal if they occur within the space bounded by the periphery of the organism. But there are difficulties to be encountered even on that basis, for it may be desirable in some cases to regard the periphery as enclosing spaces like sub-stomatal cavities and just as desirable in other cases to consider such spaces as environmental. In considering our own bodies the lung cavity may be either within or outside of the body periphery, according to the nature of our analysis or enquiry. Obviously no criteria may be established that can be wholly satisfactory in all discussions. Each particular discussion needs to conform to its own more or less arbitrary, but clearly understood, distinction between organism and environment.

Physiology deals with all the processes that go on within the organism. These may be considered in larger or smaller groups, or sometimes singly, but they are more or less related and interdependent. Without reference to its causal relations, any process or change, whether single or complex, may be described for any period of time according to its nature, its direction, and its velocity. The last two characteristics may be united as velocity if we introduce negative we well as positive values. Thus, we may say that sugar changes to starch (and a little water) in a developing potato tuber at a certain rate for a given period, the rate being stated as the amount of starch formed or of sugar used up per hour, etc. In the sprouting potato the reverse of this process goes on, starch and water become

sugar. When a change ceases altogether its velocity is simply zero. In many instances we consider processes that go on both positively and negatively at the same time and we describe them in terms of their net velocities. Thus sugar and oxygen change to water and carbon-dioxide in a typical living green leaf at all times, with evolution of free energy, but the reverse of this change, photosynthesis of carbohydrate, occurs only under adequate conditions of illumination, etc. The negative process when it occurs, generally greatly exceeds the positive in velocity; consequently, more sugar is usually formed per day than is used up. In such a case, if we consider days or weeks or seasons, we may say that the net velocity of the oxidation of sugar is negative and we may altogether neglect the positive velocity of respiration. A close analysis requires the consideration of both positive and negative rates in most cases. An infinite number of processes are truly negligible because their velocities are zero, they do not occur at all in either direction. And many processes of organisms are sometimes positive, sometimes negative, sometimes both together (with equal or unequal velocities) and sometimes wholly absent—at least as far as our measurements and present knowledge suffice.

Excepting in the very rare cases in which a process velocity is uniform for the period considered, the complete description of a change (still without taking up the question of causality) requires yet another term, to picture the *alterations* in velocity that occur. For example, the rate of transpiration from a leaf may sometimes be practically maintained for very brief periods but this rate differs markedly for different short time periods in a single day and it generally fluctuates continually. The additional term of our description is, of course, the *acceleration*, which itself may be positive, negative or zero and may be maintained or may fluctuate with time. For the simplest approach to the dynamic aspect of physiology we determine rates of change for several shorter periods in a longer period and commonly express our results in the form of the familiar plotted graph, with time intervals as abscissas and process rates or increments as ordinates. If the graph is a horizontal line the process has evidently continued at a maintained rate throughout our study. If the graph is rectilinear and slopes upward or downward we see at once that a positive or negative acceleration has been effective and that its magnitude has been maintained; that is, the rate of the process has increased or decreased uniformly with the lapse of time. Most of our graphs turn out to be curves, however, which indicates that the magnitude of the acceleration changed in the longer period of our study, and it usually happens that the acceleration not only alters in magnitude but changes its sign from time to time. Thus the rate of transpiration from a leaf may increase from dawn till ten o'clock, slowly at first, then more rapidly, and finally slowly again, after which the rate may decrease until after sundown, the decrease being first slow, then more rapid, and finally again slow. It is thus that we secure the usual daily graph of the transpiration rate, with a maximum near the middle of the day and a minimum at night. It is thus that we get the grand curve of growth. The march of the acceleration itself is frequently found to undergo accelerations and retardations of its own, and so on, and so on.

Although I seem thus far to have prepared your minds for a consideration of physiological process rates in terms of the mathematical calculus, I shall nevertheless not persist further in this direction. It may be remarked only that plant physiology has described most of its known processes in terms of nature and direction, and many of them in terms of rates or velocities also, and that the time approaches when we shall be able to add to some, at least, of our descriptions some quantitative consideration of the rates of velocity change, the accelerations. I do not imagine that accelerations of accelerations, the second and higher derivitives, will enter much into most physiological discussions for a time.

Thus far we have been thinking of describing the life processes or changes as precisely as we can, with reference only to their occurrence in time and without attention to their causal relations. The questions before us have been: (1) what changes occur, (2) in what direction does each occur, (3) how rapidly does it occur, and (4) in which direction and at what rates does it vary in the rapidity of its occurrence? Such descriptions must of course include statements of the amounts and kinds of matter and energy involved in each particular process and also statements regarding the results or products. Such somewhat detailed descriptions are prerequisite to the study of the causal relations that determine or control physiological processes, just as they are needed for the etiologlcal study of processes or changes in general. We cannot escape this necessity. They are to studies of causal relations just what the description of static conditions is to the comparative study of form, size, color, material, etc., of objects and structures as dealt with in anatomy.

But the most interesting feature of any change or process is its causation. To the four questions stated above we add a fifth: Just why does the change occur precisely as it does? For example, to employ one of the simplest of plant-physiological processes, we may have described the process of cuticular transpiration from a certain leaf for a certain day, stating (1,2) that the process in question is the vaporization of water from air-liquid interfaces where the imbibed water of the cuticle is in contact with the atmosphere (liquid water being thus removed from the cuticle while equivalent increments of water vapor are added to the adjacent air), (3) that the process is more rapid at times than at other times and (4) that it is accelerated or retarded at certain rates, according to the time of day, etc. We now ask (5) why does this vaporization occur at all, why does it not go on at a maintained rate, why, since it is observed to vary in velocity, does it increase or decrease its speed at just the times and with just the accelerations indicated by our observations? In short we ask ourselves for a descriptive statement, as complete as possible of the deterministic controls or influential conditions that are involved.

In mankind's long and slow progress toward an appreciative knowledge of the world, the question of causation seems usually to have been prominent from the very first observation of any process, and that question generally looms very large in all present-day scientific enquiries. Indeed, the desire for a better knowledge of controls in nature is, among many men of science at least, the main impelling urge toward the development of improved means and methods by which

changes may be described. We find that our interest in the question "why" often outstrips our interest in the question "what" and "how" and we frequently need to go back and improve our "what-how" description before we can proceed with our "why" discussion.

The application of scientific knowledge in the arts furnishes a strong additional impulse toward the study of processes with regard to their controlling conditions, for if we can understand these controls we may not only make true predictions but we may in many cases tame the processes and make them go on as we wish. This impulse is evident at nearly every turn in plant physiology. Whether for the sheer pleasure of the deeper appreciation of things, or for the easier attainment of our daily physical needs and wants, or for the acquisition of wealth and property and position among our fellows, the greatest satisfaction comes from an understanding of causal relations. *Felix qui potuit rerum cognoscere causas.*

The study of causal relations is of course based on concomitancy. If two or more changes are always observed to happen together, or if a given change is always preceded by one or more other changes, then we say a causal relation is probably involved. In physiological study concomitancy of rates of change is of primary importance. Those whose data allow the application of statistical methods for determining degrees of correlation between physiological processes and other changes, or between different physiological processes, readily secure numerical measures of concomitancy; but indices of correlation are very apt to be misleading, for the causal relations of physiological processes are generally not simple. There are usually a number of influential conditions and the concomitancy is not between single and simple processes or changes; it is rather between the rate changes of the process considered and an integration of the rate changes of many other phenomena all of which are influential.

A discussion here of causality and the sorts of evidence upon which we may consider it relatively well demonstrated would carry me too far afield from my present topic, and I shall be obliged to content myself in this connection with a few remarks about the integration of influential environmental conditions as required in physiological and ecological study.

The activities of the organism are themselves integrations or summations or resultants of many physiological processes, all of them fluctuating more or less with time. The environment contributes the influence of many other changes and the results of these influences inevitably enter into the physiological integration. Our first task is to find out what ones of an infinity of changes are influential on the particular activity that we are considering. This is difficult, but if the influential conditions had already been correctly selected we should be confronted with a still greater difficulty; namely, the problem of weighting and summing them in such a way as to render our own integration comparable with the natural integration furnished us by the process itself. Of course we must also be able to read and express this natural integration in adequate terms. Frequently a relatively simple process is very difficult to interpret in terms of its influence on an organism. For example, there is a sort of concomitancy between the rise and fall of a thermometer meniscus and the rate of elongation of the plant stem,

with other conditions suitable for elongation, but the rate of stem elongation is far from being proportional to thermometer changes, even when no influences besides temperature are supposed to be active. Indeed a rise in temperature is sometimes followed by more rapid and sometimes by less rapid elongation, other influential external conditions remaining the same. The best that we can do is to seek to measure and weight and integrate influential influences in ways that will give us numerical indices that are shown by experiment to be comparable with the physiological rate changes with which we are dealing, these being themselves resultants of all the influential conditions, both internal and external.

The changes that go on in an organism are numerous and multiform and it is of course, practically impossible to deal with them separately in most cases, even in the simple descriptive manner, because we are as yet generally unable to gain an adequate knowledge of details. We generally deal with large groups or systems of changes, such as respiration, photosynthesis, enlargement, transpiration, absorption, wilting, etc., or with still larger systems. It is thus far only with a few of these larger groups that serious and consistent attempts have been made to work out analytical statements, even without much attention to causation or control. With the largest groups, however, a great deal has been done. I refer to such process complexes as growth, production of seed, production of certain compounds like acids in fruits, etc.—complexes with the results of which agricultural science is vitally interested. The innumerable and mostly still unmeasurable component processes that make up growth, for example, do automatically become integrated into complex processes that can be measured as such in many ways and with relative ease. No one can yet describe with any satisfactory degree of detail just all that goes on in a wheat plant between seed germination and harvest, but there are available fairly satisfactory ways of measuring the seed planted and the crop produced.

That we need to deal with the organism as a whole, or with large and complex parts of its system, need not, however, be discouraging. We may remember how recently attention has been directed to such things and how much has already been accomplished, as demonstrated notably in recent agricultural and horticultural methods. The behavior of a plant as a whole may be fairly well understood in many respects without much knowledge of the many particular changes that together constitute that behavior. Much may be known about molecules without a knowledge of atomic behavior. Atomic behavior was long understood in many respects and to considerable degree without any insight into the behavior of electrons.

It is the larger groups of physiological processes, the larger physiological complexes, and especially the more obvious and measurable changes of the organism as a whole, that we may best study at present, if we hope to make progress with respect to the causal and determining relations between the internal complex and the surroundings. A host of external conditions are in operation, but fortunately most of these are without notable influence, and we consequently need to consider only the influential conditions or those that seem likely to be

influential. Conditions that are only indirectly influential on the process in question may be neglected if we can include their indirect effects in our study of directly influential conditions. But that is just what we are usually unable to do at present, and these statements of mine savor strongly of an ideal not yet nearly attained for most physiological enquiries. Still, it is stimulating and encouraging and clarifying to try now and again to see whether the concept of antecedent causation is to lead in our persistent attempts to learn to understand and control plant changes.

It is well-nigh axiomatic in present-day science, and in ordinary affairs as well, that every process has its antecedent set of causal conditions and also its subsequent set of results or products. Perhaps the primary article in the practical faith of an experimenter is that these three things, (1) antecedent influential conditions, (2) change or process, and (3) results, are somehow fundamentally and inevitably joined together. Given the result, we are sure there must have occurred a process; given a process, we are sure that there must have been a causal complex and that there must be a result; given a proper set of antecedents, we are sure there must occur a process and results. This article of our creed is seldom dwelt upon, being taken for granted like an axiom, but it is of very great importance in biological study and its necessary corollaries are not infrequently neglected in what is sometimes mistaken for scientific reasoning. It should be noted, for instance, that a specified set of antecedents must always cause the same process and result, but that any specified result may be brought about by any one of several different or many sets of antecedents.

This is the place where I should say some derogatory things about the strange and wierd views of teleology, seen—and sometimes apparently enjoyed—when one looks upon the world with one's mind upside down. In such views the result is considered as the causal complex, which necessitates the process that brings it about, and the process itself appears to necessitate its antecedent conditions. However much momentary thrill and mystic wonder or philosophical pleasure may be derived from thus standing on one's head while attempting to study the processes of living things, I am sure that physiological experimenters do not generally rely on such inverted views in the planning and interpretation of their experiments. Our experimental science rests conformably upon the common-sense concepts by which ordinary daily affairs are considered, and it is on the basis of common sense that physiology is to progress. We who are trying to further its development need not worry much about the inverted view, excepting to bear in mind that it is still at large in the world of scientific thought.

The antecedent conditions that necessitate and determine the changes of an organism are of course really all active within the organism. As long as radiation or molecular vibration, substances like carbon dioxide, ether, or potassium nitrate or gross mechanical movements like those of a rodents teeth, are entirely outside of the organism they are without direct effect in altering its processes. But each influential external influence reaches into the organism in some way and sets up an internal change, which, in turn, becomes an influence for further changes inside or out. It is difficult to think of measuring most of these internal influences

but we have made much progress in measuring and comparing the corresponding external conditions. We consequently take our position at the periphery of the organism and look both inward and outward, in our search for the antecedent controls that are implied by the occurence and rates of physiological processes. As has been said, although the environment and the organism are truly continuous and parts of a larger system, we find it practically advantageous to regard them as two separate systems with continual interchanges of matter and energy, and with inevitable influences to and fro.

I suppose the true province of physiology, when considered from an ideal point of view, extends outward just beyond the periphery of the organism. Physiological interest in the environment ideally begins or ends just when and where the influences of the environment impinge on the organism, just when and where those external influences begin to influence, just when and where they, or their immediately resultant effects, become internal influences. But we are generally not able to appraise these impinging environmental conditions just as they impinge, and we are forced to make our examinations of them more or less farther out. As well as we may, we aim to catch them in the net of our experimentation and instrumentation just before they impinge. In many cases we need to extend that net far into the outer space of the environment and in many instances we need to deal with secondary or tertiary, etc., controls rather than with ideally immediate conditions. For example, we have related plant growth to precipitation data or even to latitude or the vicinity of mountains or of the sea, although we are well assured that these things have no direct influence on the life processes of plants. They are conditions that take part in determining other conditions, and so on, like the story of the house that Jack built, until a critical link in our chain of influences and effects touches the organism and the next influence reaches into the interior.

The analytical approach toward a dynamic and deterministic picture of a life process (whether very complicated, like growth and development, or relatively simple, like transpiration) involves measurements of the process itself, measurements leading to the sort of simple description upon which I have dwelt at the beginning of this paper, with reference to material and energy changes and to time, and it also involves measurements and proper integration of both the internal and external complexes as they influence the process. In the most perfect forms of experimentation we try to produce the environmental complex artificially, although we generally succeed only in part. If an environmental feature or characteristic is artificially produced its measurement is in many cases unnecessary, for the operation of producing it may have given the quantitative imformation that would otherwise have had to be derived from measurement. Thus, if a simple salt solution is properly prepared we do not need to analyze it in order to find out what proportions of salt and water it contains. But measurement is generally necessary with artificially produced environmental features that are at all complex, for we may know what we put into a mixture without knowing just what may be there when we have done. In the most thoroughly controlled experimentation unknown influences are generally to be suspected; some effective

conditions remain still not well enough known for our analysis. And natural environments always confront us with problems of measurement.

Unknown influences, only the effects of which we can measure and consider analytically, form a large but surely diminishing portion of our hypothetical systems of deterministic controls. To escape temporarily from the mental irritation of contemplating effects for which we have not yet found relatively satisfactory explanations, we put such things away in a handy category labeled unknown variables, chance influences,—the sorting activities of demons, or the acts of some *elan vital* or complex of entelechies or other more or less nicely fabricated supernatural powers, according to our artistic taste in such matters. But we of course realize that this manner of disposal has only temporary use,quieting our mental pains as does a narcotic or anaesthetic and thus permitting us to proceed with our analyses in terms of the influential conditions that are better understood. The unknown influences present inevitable problems, however, and we must sooner or later come out of our self-imposed narcosis or hypnosis and undertake their solution, one after another. –

If we can do no better, the influence of chance (that is, of unknown conditions) may sometimes be located with reference to our two primary systems, the organism and the environment. A certain control or group of influences that has thus far escaped us may be shown experimentally to be either internal or external. If this step can be taken much has already been accomplished. Furthermore, chance is not omnipotent and its insidious action is, for any particular analysis, confined within intensity limits that may be determined by statistical methods for a group of organisms or of environmental complexes.

Every study of the causational aspect of plant behavior inevitably involves measurements of the capacity of the organism to respond or to be influenced, as well as measurements of environmental influences.

It is logically possible in many cases to consider all the influential internal conditions together and to regard the process with which we are dealing as itself a key to them. The resultant of the process is measured for a time period, the environmental influences are measured, (in proper terms) for the same period, and we say that this organism, operating under the stated external influences, is capable of carrying on the process in question at a stated rate. By studying the same organism under the same environmental conditions for different times we get information as to how the internal capacity may change with time. By employing different environmental complexes with different but like organisms at the same time we secure indications as to how the internal capacity differs with differences in the surroundings. It is thus possible to make much progress without looking into the organism at all, excepting to measure and describe the particular process we are studying, in terms of its resultant or products. But this general method cannot lead beyond simple description unless we have adequate quantitative indices of the environmental influences and adequate methods for integrating these with respect to their bearings on the process in question and for the time periods involved in our study.

In default of more analytical and better methods, we may compare the capaci-

ties of different environmental complexes, by employing originally similar organisms as automatically integrating instruments. What a plant can do is what its internal characteristics allow to occur under the current influence of the external complex, and that is exactly what it does do. From this emerges the suggestion that standard plants may be used as instruments for environmental comparisons, a method employed by plant growers from the beginning, and recently with increasingly scientific results. This suggestion was made for theoretical ecology and physiology by Livingston and McLean[2] and the method has been elaborately worked out for ecology by Clements and Goldsmith[3]. The principle involved is, of course, commonly employed in physiological experimentation, especially in the use of experimental controls. One of the greatest difficulties in obtaining satisfactory standards of reference lies in securing adequately similar organisms, with adequately similar internal complexes. At present our best method is to select our organisms for likeness by as many indicative criteria as possible and then to use large numbers for each test, applying simple statistical methods to test the significance of resulting differences. In any event, the results and conclusions apply only to the particular group of organisms used or to other groups like them, and if these organisms cannot be defined so as to make possible the securing of others like them our experimental work is correspondingly unsatisfactory. The same is true of any sort of instrument for measuring and comparing things of any sort. If my meter stick is not essentially like yours we may measure a table with ever so great precision and still have discordant results, with apparent grounds for suspecting each other of poor work.

This line of thought leads to two general propositions: (1) that different internal complexes (of different organisms at the same time or of the same organism at different times) may be compared for a given external complex; and (2) that different environmental complexes may be compared (for different locations at the same time or for the same location at different times) for a given internal complex. We need a suitable standard of reference in every case, however, and that renders the application of these principles fundamentally difficult at present.

It is common to consider the plant or other organism with which we may be interested, as a dynamic system, as a machine which takes from the environment material and energy, transforming them in various ways and finally letting them go again. The physiological processes consitute the operation of the machine or system. It is not so common to consider the environment as another, much more extensive machine, linked variously to the organism and inevitably operating with it. This point of view seems to me to have much promise. Can we not treat the environment also as a machine, delivering material and energy to the organism in manifold forms and at manifold and varying rates and removing, also at manifold and varying rates, the material and energy that leave the organism?

[2] Livingston, B. E., and F. T. McLean. A living climatological instrument. Science 43: 362. 1916.

[3] Clements, F. E., and G. W. Goldsmith. The phytometer method in ecology; the plant and community as instruments. Carnegie Inst. Washington, Publ. 356. 6+106 p., 45 *fig.*, 11 *pl.* Washington, 1924.

As in any other operating system, the processes of any individual organism go on according to the rates at which material and energy become available and according to the rates at which freed energy and material are removed. These rates are the influences or antecedents that necessarily determine any process. As we well know, some of them are internal, while others are effective from the outside, and we have generally agreed to consider these two groups of rates as separate for the purpose of general dynamic and deterministic analyses. It is to be remembered, however, that the internal system is not a static affair and that it may maintain the vital processes long after some of the environmental supplies may have become apparently inadequate; there may be, in some cases, a pronounced lag in the effect produced on the organism by the incidence of an inadequacy or other alteration in the environmental processes. The activities of the environment represent work, just as do those of the interior, and their kinds and rates are partly determined by the configuration of the internal conditions of the organism; the organism often operates to retard or offset the influence of its surroundings.

Now, it should be possible to appraise and compare different environmental complexes according to, and in terms of, their capacities to supply material and energy to the plant, just as the water power of a stream or mountain lake may be determined, or the heat producing power of the sun or of a pile of coal. I think sufficient progress in this direction has been made so that we may be sure this is an excellent method of approach to our general physiological and ecological problem. The point of view and the units employed are somewhat different from those generally in vogue and I wish to place before you a sort of preliminary discussion of some of the possibilities of this proposal.

In the first place, we need to be careful to hold constantly in mind the interaction between the external and the internal systems. Neither system can operate without the other. To illustrate, the water power of a lake is not applied to the water-wheel and other machinery of a mill unless these machines have the capacity for using the available power. Other conditions having been properly adjusted the mill may be idle or may operate at various speeds, up to the limit set by the available water power, but if the miller wishes to surpass that limit he must alter conditions outside of his mill (as by increasing the height of his dam or drawing on a larger supply of water) or else he must secure more efficient machinery, or he may do both these things together. As long as the environmental power is adequate for the given machinery the rate of operation of the mill is dependent only on mill conditions. So, a given plant may utilize to a certain degree what the environment supplies but it can not utilize material or energy at a rate greater than that at which these are, or have been, furnished by the surroundings. Of course the plant stores absorbed material and energy and utilizes these at later times, but the processes of storage are themselves physiological and they can not proceed unless the surroundings furnish what is stored as well as what is currently used. Indeed storage is a form of use. Stored energy and material are internal conditions that may or may not be effective to influence any given physiological process.

Taking the water-supplying power of the soil[4] as an example of an environmental capacity, the supply of water to the absorbing surfaces of the root system is generally (with healthy plants) much greater than the absorbing power or absorbing capacity of the roots, and the rate of entrance of water is then limited directly by internal conditions alone. Only when the internal absorbing power is greater than the external supplying power does the latter generally become a limiting or influential condition. Ordinary lawn grasses in Baltimore in summer thrive as long as the index of the initial water-supplying power of the soil is above 100 at a depth of 5 or 6 centimeters (soil-point method with one-hour exposures) and the leaves of these plants promptly become brown when the index of initial water-supplying power is as low as 40 or 50. An index value of 100 corresponds to a possible rate of delivery of 100 milligrams of water for the first hour at a surface of 12 square centimeters, or about 8 milligrams of water per square centimeter of absorbing surface for the first hour. With a supplying power of 40 the leaves dry because the environmental system cannot supply water as rapidly as it might be used, for the roots could absorb that substance at a greater rate if it were supplied. In such a case we may be sure that the limiting conditions are not internal but are external.

However, the internal conditions may be the limiting ones when a plant is injured. A plant may wither with its roots in free liquid water (supplying power practically infinite) if the water-absorbing power or water-conducting power of the plant itself are not adequate to the current transpiration rate. It is clearly essential that we generally study both supplying power and absorbing power, both the external system and the internal one.

My proposal is that we set about to make dynamic descriptions of the influential environmental capacities as far as we can, as well as of the internal capacities or powers of the plant. I am sure that such descriptions will profit physiology greatly and will place in our hands means for great progress. But we shall need new concepts and new methods, and new units will need to be devised. The project is not a simple one, but static descriptions have already proved themselves to be inadequate. The great present need of biology in general is to develop the dynamic aspect of the relations between living things and their surroundings.

To secure a preliminary outline of the field to be cultivated with respect to environmental conditions, it is convenient to consider separately the aerial and the subterranean portions of the environment of an ordinary plant. We may speak

[4] Livingston, B. E., and Riichiro Koketsu. The water-supplying power of the soil as related to the wilting of plants. Soil Science 9: 469–485. 1920. Mason, T. G. The physiological humidity of the soil and its direct determination. West Indian Bul. 19: 137–154. 1922. Hardy, M. A. The soil-point method for directly estimating the water-supplying power of the soil in a field. Jour. Agric. Sci. 13: 355–360. 1923. Livingston, B. E., and Ichiro Ohga. The summer march of soil moisture conditions as determined by porous porcelain soil points. Ecology 7: 427–439. 1926. Livingston, Burton E., Takewo Hemmi, and J. Dean Wilson. Growth of young wheat plants in auto-irrigated soils, as related to the water-supplying power of the soil and to the adjustment of the auto-irrigator. Plant Physiology 1: 387–395. 1926. Wilson, J. Dean. The measurement and interpretation of the water-supplying power of the soil with special reference to lawn grasses and some other plants. Plant Physiology 2: 385–440. 1927.

of these as aerial conditions and subterranean conditions. They are the influences that impinge directly upon the top and the root system, respectively. It is also convenient to consider separately the supply and removal of matter (with the potential energy that it carries) and the supply and removal of energy as these occur without transfer of matter. The first of these last two categories of transfer includes processes of flow and diffusion, the last includes processes of conduction and radiation.

The aerial surroundings deliver to the organism, under usual conditions, carbon-dioxide, oxygen, water, conducted heat and radiant energy (mainly solar radiation, direct or reflected). They receive from the organism and dispose of the same things. For plants growing in the open we are especially interested in the environmental supplying powers for carbon dioxide, conducted heat and radiation. The oxygen-supplying power of the air is high and probably always adequate under such conditions. The water-supplying power of the air is negative excepting in periods of condensation and heavy precipitation; the aerial portion of the environmental system acts mostly to remove water from the plant.

The carbon-dioxide-supplying power of the air is not generally measured and we know but little about it as yet[5]. We know that it differs for different locations (being higher near the soil surface than farther up, especially when the carbon-dioxide-supplying power of the soil is high, and sometimes higher with wind than without). Among crowded green and healthy leaves it is apt to be appreciably higher by night than by day, other conditions being the same for both periods. These natural differences are relatively slight and may possibly not be important in determining plant growth, etc., in nature, but this feature frequently requires very careful attention when plants are subjected to experimental conditions. It has been shown by a number of experimenters that a proper increase in the carbon-dioxide supplying power of the air on bright days may result in an increased rate of production of carbohydrates by many kinds of plants. Aside from the influence of air circulation (which must be of considerable importance) this environmental supplying power may perhaps be taken as proportional to the partial pressure of carbon dioxide in the air, a static feature of the environment. With higher internal partial pressures of carbon dioxide the process is reversed and the environment removes this substance from the plant, as from active leaves at night. (It should be noted that the possibility of much carbon-dioxide absorption by the roots, with water from the soil, is recently becoming prominent).

The capacity of the air to remove water vapor from the plant has been called the evaporating power of the air[6]. It depends on the water vapor-pressure deficit and air circulation and it can be measured in a general way by means of atmometers of various forms. From a spherical evaporating surface 5 centimeters in diameter the air is capable of removing as much as 15 or 20 grams of liquid water

[5] Livingston, Burton E. Carbon-dioxide supplying power of the air. Carnegie Inst. Washington, Year Book **20**: 71–72. 1921.

[6] Livingston, B. E. Atmometry and the porous-cup atmometer. Plant World **18**: 21–30, 51–74, 95–111, 143–149. 1915.

per hour for the driest hours of the driest days in the driest regions. The air of ordinary laboratory rooms is considered comfortable for human beings, as far as this feature is concerned, when it removes one gram of water per h ur from the standard spherical surface. When this capacity is negative dew and fog form through condensation.

This environmental capacity must not be thought of as an absorbing power of the atmospheric gases, as it is sometimes pictured. It is really the capacity of the aerial surroundings to allow the vaporization of liquid water and the further movement of the vapor away from the evaporating surface, as these processes tend to occur, and to accelerate them through the delivery of heat to the evaporating surface and the adjacent air, largely by conduction. It is convenient to consider radiational influences on evaporation separately, as an additional condition promoting the vaporization of water and the outward diffusion of water vapor, but this may be combined with the evaporating power of the air when such a combination is desirable.

The radiational influence of the surroundings, which in nature usually emanates directly or indirectly from the sun, may be measured as a whole, or in parts corresponding to certain ranges of wave-length. Various forms of radiometric instruments may be used, but the available methods are not nearly all that is desired. The total radiation at mid-day in June at Tucson, with clear sky, may be sufficient to increase the hourly vaporization of water from our standard spherical surface by 2 or 3 grams. The radiation influence on plant transpiration is often much greater than the air conduction influence, the sunshine effect being in such cases greater than the evaporating power of the air. The great importance of certain wave-length ranges of radiation for photosynthesis is well known.

The energy supply through conduction from the air is mainly related to the temperature of the air and of the plant leaves, but the positive radiation influence is not usually thus dependent, within the limits of natural conditions. Radiation may be intense for considerable periods when both plant and air are relatively very cold. Thus, sunshine may greatly accelerate the evaporation of ice without appreciably warming the adjacent air. Air movement promotes conduction but is without influence on radiation.

Large amounts of heat are removed from the plant not only as the latent heat of water vapor set free by transpiration, but also by conduction to the air and to some degree by outward radiation. It is probable that radiation is of but little importance in the direct removal of kinetic energy from the plant, however. So far as I know, little has been done toward the dynamic study of these energy relations of plants. Indeed, the processes of conduction and radiation are frequently very badly confused in current discussions. This is a field of great promise, for we are sure that heat supply and light supply are of the utmost importance to ordinary plants. The method of the katathermometer, as used by students of hygiene and human ecology, is an important lead in the direction here suggested. The electrical relations between plant and air have received some study, with uncertain results, and this subject will surely be followed further.

When aerial supplying powers are too great the plant often absorbs more

matter or energy than is good for it and thus becomes injured or killed. Many poisons may thus be driven into the organism by an environment too active in their supply. In such cases the internal system does not resist sufficiently the entrance of the injurious substance. On the other hand, harmless substances like nitrogen, helium, or hydrogen may enter or leave the organism without noticeable effect on the life processes, according to their diffusion gradients and the resistances offered by the internal system.

Turning to the subterranean environment of the ordinary plant, we find another complex and difficult state of affairs. Through its root system the plant receives from the soil complex large amounts of water, considerable and essential amounts of a number of chemical elements or their ions or compounds, including considerable amounts of oxygen and carbon dioxide. It also doubtless receives from the soil a large amount of heat by conduction but perhaps practically no energy by radiation. Yet electrical adjustments by energy transfer between soil and plant (as well as between plant and air) may prove to be important as our science progresses. Considerable heat is surely given out by growing roots,etc.

I have already briefly discussed the water-supplying power of the soil, which is one of the most important of the dynamic environmental influences, and we need not dwell on it here. The oxygen-supplying power of the soil has begun to receive attention, as is attested by the recent work of Hutchins[7] and of Cannon.[8] It seems to be fully as important, for many plant forms at least, as is the water-supplying power. The apparatus and technique of Hutchins will be very valuable to ecologists and other students of the soil-plant relation. Other conditions being adequate, rice seed germinates in soil that cannot supply oxygen more rapidly than 0.5 mgm. per square meter per hour, and wheat seed appears to require for germination a supplying power of 2.5 or 3.0 mgm. per square meter per hour.[9]

How important the carbon-dioxide-supplying power of the soil may be remains still to be looked into. With suitable modifications, the Hutchins method should be useful whenever this question is to be taken up. In this connection it should be suggested, however, that both oxygen and carbon dioxide, as well as other dissolved substances in the soil solution, may perhaps sometimes enter the root system by flow as well as by diffusion. The soil solution may, under some conditions, flow into the absorbing organs, carrying with it any contained solute particles that are not prevented from entering. This is an interesting and fundamentally important question, which should receive more attention than it has received. It may be that flow is not important in any case, but it should not be ignored without experimental basis. At any rate, it seems likely that large

[7] Hutchins, Lee M., and B. E. Livingston. Oxygen-supplying power of the soil as indicated by color changes in alkaline pyragallol solution. Jour. Agric. Res. 25: 133–141. 1923. Hutchins, Lee M. Studies on the oxygen-supplying power of the soil, etc. Plant Physiol. 1: 95–150. 1926.

[8] Cannon, W A. Experimental studies on roots. Carnegie Inst. Washington, Year-Book (1924–25) 24: 289–298. 1925. Idem. Physiological features of roots, etc. Carnegie Inst. Washington, Publ. 368. Washington, 1925.

[9] Livingston, Burton E. Dynamic relations between plant and soil, with special reference to the supply of water and oxygen. Proc. Natl. Acad. Sci. 14: 293–295. 1928.

amounts of carbon dioxide are absorbed from the soil in one way or the other, during periods of high rates of water absorption.

The dissolved molecules and ions that are called plant-food by many workers in applied plant physiology (these particles being derived from the salts, etc., of the soil) and many other kinds of material that may be dissolved in the soil solution, are supplied by the soil system. Numerous studies on the amounts of potassium, calcium, and other ions etc., in the soil have been carried out, but in such studies the problem must be treated as one of statics. Just as a soil may contain large amounts of water per unit of volume and still have only a low water-supplying power, so it may be that a soil containing large amounts of potassium, for example, may still have but a low potassium-supplying power. This suggests at least six or seven supplying powers that should be studied, but methods for such dynamic studies of mineral supply remain to be devised.

It has been mentioned that injurious substances may enter the plant from the air. A similar statement applies to the soil. Toxic substances may be driven or carried into the root system if they are present in the adjacent soil solution and if they are not prevented by special conditions, partly related to specific permeability in the absorbing organs.

That conducted heat migrates from soil to plant and from plant to soil is perfectly clear, but how much energy the plant gains or loses by this means is only a matter for conjecture. Just as a great deal of attention has been devoted to air temperature as an environmental feature, so there have been some excellent studies on soil temperature as it is related to plant growth. These studies of environmental statics are important but they need to be supplemented by studies from the dynamic point of view. No attempts have yet been made to study the heat-supplying and heat-removing power of the soil, which must vary with the kind of soil and its degree of compactness as well as with its water content and temperature. I think that even the katathermometer has not yet been applied to soil studies.

Conclusion. The topic I have asked you to consider in this preliminary way is complicated and seems difficult at present. This is due to the innate complexity of the causal relations between organism and environment and to the fact that the dynamic features of these relations have only recently begun to attract serious attention. I am sure, however, that both theoretical and applied plant physiology will be advanced a great deal as the dynamic point of view is more generally taken. It is especially important that the whole world be looked upon as a complex of fluctuating processes or changes, of which the activities of our plants and of all organisms must be component parts. As physiology advances, the relations of dynamic causality will become more prominent and capable of more satisfactory treatment in our biological discussions. What seems to be most needed at the present time is methods and instruments suitable for evaluating and comparing and integrating the many influences or conditions that work together to make the plant what it is and to make it do what it does

CHEMICAL PROBLEMS IN ALCOHOLIC FERMENTATION[1]
(Abstract)

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Prior to the investigations of E. and H. Buchner a chemical fermentation problem, in the sense of being independent of complicated "vital" processes, could scarcely be thought of. The chemical course of fermentation constitutes now one of the largest fields in modern biological chemistry. The problem of alcoholic fermentation presents enormous difficulties because the process obviously proceeds in many stages, the phases of which are closely coordinated; and, further, the first stages are related to space arrangements of the atoms in the sugar molecule, concerning which our information is far from complete. The influence of phosphates and the great significance of hexosephosphates in cell-free fermentations have been demonstrated. It would appear definite that all fermentable hexoses form a common hexose-phosphate-ester which later yields other products of fermentation. The author approached this problem with full appreciation of the reduction-capacity of yeasts and of the significance of the formation of the corresponding aldehyde when CO_2 is split off from the alpha ketonic acid, also considering many other facts of interest in this connection. Moreover, in his own investigations it proved simpler to consider first of all the end-products and their intermediate stages rather than devote first attention to the complicated beginning stages. Regarding ethyl alcohol, it may be assumed that this arises from acetaldehyde, and convincing evidence has accumulated showing the production of acetaldehyde in sugar fermentation; likewise, evidence establishing the relation, by reduction, of acetaldehyde and ethyl alcohol. For reasons clearly advanced, the author does not define the whole process as a reduction of aldehyde to alcohol. Later developments, especially the introduction of the sulphite method, into yeast fermentation, whereby perhaps glycericaldehyde and later glycerin are produced, have become well known. With due consideration of the extensive later work of Neuberg and his associates, the author concludes that his own work established not only theoretically but also experimentally the formation of acetaldehyde from sugar. Moreover, recent work in his laboratory has confirmed earlier findings regarding the specific action of zinc and cadmium ions upon plant ferments. Pyroracemic acid is undoubtedly an intermediate fermentation product, and the production of alcohol and of CO_2 are two separated reactions. Further, acetaldehyde is reduced as a result of the

[1] Presented before the International Congress of Plant Sciences, Section of Physiology, at Ithaca, New York, Aug. 17, 1926. (Editor's note: The abstract is by the Editor. It is hoped that this paper will be published in full elsewhere; it is omitted because of practical difficulties.)

liberation of active hydrogen. Theoretical assumptions alone are available in regard to the first phases of fermentation. A probable view is that the hexose chain is split into two chains each of three carbon atoms. The intermediary formation of glycericaldehyde is also probable. The course of the reaction based on Neuberg's theory of the formation of methylglyoxal is presented in detail, but it is pointed out that certain of the reactions in this scheme could not conceivably be regulated outside the living cell. Undertaking then to build a working hypothesis as to how pyroracemic acid is formed from sugar, he would first emphasize the coordinating action of several ferments, and in the early stage of hexose fermentation the probable coordination of phosphatase and zymase, later of reductase, carboxylase, and mutase. A detailed scheme of reactions was given showing various phases that may be assumed, or analogies that make these seem probable, the whole process being characterizable as simultaneous oxidation and reduction.

PENETRATION INTO AND THROUGH THE PROTOPLASM[1]

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Although the penetration of substances into and through the protoplasm has long been recognized as an osmotic process we sometimes hear statements pointing out some contradictions persisting after the assumption of the identity of both processes. The improved methods show, however, that these contradictions owe their existence either to mistakes or to our lack of acquaintance with the phenomenon of osmosis itself. One must confess that this phenomenon has not been adequately investigated quantitatively. The adsorption of substances by colloidal membranes can modify the rate of osmosis only at first, and as soon as the adsorptive power of colloidal membranes is satisfied the penetration proceeds corresponding to diffusion laws.

Since the protoplasm must be regarded as a colloidal system, the penetration of substances into and through it can be compared with those through artificial colloidal membranes, but one must always remember that the active protoplasm is fluid, and that its surface is generally not covered by any semipermeable sediment-membrane (plasma membrane). Since the diffusion rate depends on the mass or volume of molecules, or particles of dissolved substances, and on the internal friction on passing through the medium, every liquid layer may be regarded as an ultrafilter or as a molecule-sieve. In this sense the protoplasm might also be regarded as an ultrafilter.

The principal difference between the diffusion through the protoplasm and that through an artificial colloidal membrane (for instance, through a sediment-membrane of copper ferricyanide, or gelatine) lies in the difference of the solvents in the two cases. While in the first case the solvent is a molecular mixture of water and organic substances consisting of proteids and lipoids, in the second case the solvent is only water. Thus water-soluble substances, to penetrate into the protoplasm, must dissolve in this mixture. The more water the protoplasm contains the more, therefore, is the penetration-rate of water-soluble substances through it. On the other hand, all agents which alter the quantity of water in the protoplasm influence, correspondingly, the penetration. But lipoid-soluble substances are much more soluble in the above mentioned mixture than water-soluble substances, and their penetration either does not depend on the water content of the protoplasm or depends on it in an opposite sense. These substances dissolving in the protoplasm lower the solubility of water-soluble substances in it. The penetration of the latter, if they do not dissolve in lipoid-soluble substances, decreases, and conversely, it increases if the penetrating substances dissolve in them.

[1] Abstract of paper presented before the International Congress of Plant Sciences, Section of Physiology, Ithaca, New York, Aug. 18, 1926.

THE ANALOGY BETWEEN PLANT TISSUE AND A PROTEIN[1]

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It is my desire to call your attention to the analogy which exists between plant tissue and a single protein and to point out the importance of this analogy in the physiology of the organism. I will emphasize in this connection the work accomplished in the Botanical Laboratories of the University of Missouri with the assistance of Dr. Irl T. Scott, Dr. Ouida Abbott, Mr. E. E. Naylor, Miss Edna Kobs, Mr. Karl Petsch, Mr. Roy Campbell, and Mr. George Peckham. While emphasizing the investigations at the University of Missouri, I do not fail to appreciate similar excellent and important work which has been accomplished or is under way elsewhere. Time will prevent my reviewing it in suitable detail.

A notable advance in our knowledge of the chemistry and physics of that important group of substances, the proteins, was made by Hardy ('00). He found that the direction of movement of a protein in an electric field is determined by the reaction of the fluid in which it is suspended. Since a hydrosol in which the particles are electro-positive can be changed by the addition of free acid until the particles become electro-negative, it is evident that there must be some point, some hydrogen-ion concentration, at which the particles and the fluid in which they are immersed are isoelectric.

The significance of this point,[2] the isoelectric point, for the physical and chemical properties of proteins has been pointed out by Hardy, Proctor and Wilson, Bogue, Lloyd, Pauli, Michaelis, Loeb ('22), and others. As described by Loeb the physical properties of such a protein as gelatin are at a minimum at the isoelectric point. Thus if the swelling of the same quantity of gelatin in solutions of different hydrogen-ion concentrations is measured, it is found that the swelling is least at the isoelectric point, pH 4.7. In solutions of greater acidity or alkalinity than this, the swelling increases. The same is true for the viscosity, osmotic pressure, conductivity, and alcohol number of gelatin. According to Loeb a protein can combine with anions only on the acid side of the isoelectric point, and with cations only on the alkaline side of the isoelectric point. In other words, a protein may act as either a base or as an acid, the reaction of the solution with the isoelectric point as the critical one determining which it shall be.

[1] Presented before the International Congress of Plant Sciences, Section of Physiology, Ithaca, New York, Aug. 18, 1926.

[2] This may be a zone or range of hydrogen-ion concentrations rather than a point. (See Michaelis '22.)

Proteins are important constituents of the living substance of plants and we have been interested, in the botanical laboratories at the University of Missouri, in determining whether plant tissue is affected by hydrogen-ion concentration in much the same way as is an amphoteric compound such as gelatin, in how far the analogy between plant tissue and such a compound might hold, and the importance of such relations in the physiology of the organism.

From the brief discussion given above it is evident that there are available several methods of determining the isoelectric point of a protein. It may be determined by the method of Hardy, that is, by observing the migration under the influence of a weak electric current, of particles of the protein suspended in solutions of different reactions. It may also be determined by measuring the swelling, viscosity, osmotic pressure, alcohol number, or electrical conductivity of the protein. It may be determined by finding at what hydrogen-ion concentrations cations, or at what hydrogen-ion concentrations anions do or do not combine with the protein. Particularly useful in this respect are the acid and basic dyes. The former have colored anions and will therefore be absorbed and retained by proteins at reactions acid to their isoelectric points; while the latter, having colored cations, will be absorbed and retained by proteins at reactions alklaine to their isoelectric points. Finally, the isoelectric point may be found by determining the influence of a protein upon the reaction of the solution in which it is immersed. A protein changes the reaction of solutions in which it is placed toward the isoelectric point, making solutions which are acid to the isoelectric point more alklaine and solutions which are alkaline to the isoelectric point more acid. We have applied to various plant tissues one or more of three of these methods, namely, water absorption or swelling, absorption of cations and anions, and the influence of the tissue upon the reaction of solutions in which it is placed. The plant tissues we have used, including potato tuber tissue, Elodea, soybean root tips, and the mycelium of various fungi, respond with certain exceptions like amphoteric compounds with isoelectric points within the range of reactions compatible with life.

Isoelectric Point for Potato Tuber Tissue

Potato tuber tissue responds much like a protein with an isoelectric point in the vicinity of pH 6.0–6.4. Thus, when discs of potato tuber tissue approximately 1 × 15 mm. were immersed in buffer mixtures composed of H_3PO_4 and NaOH, secondary Na citrate and NaOH, or KH phthalate and NaOH the change in weight plotted against the H–ion concentration of the solutions produced a bimodal curve (Robbins '28). With the H_3PO_4–NaOH series the minimum between the two maxima was located at pH 5.8–6.0; with the citrate series it was found to be at from pH 5. 5–5.7; and with the phthalate series the minimum lay at pH 6.2–6.25. In later experiments with the phosphate buffer mixtures in which the solutions were kept uniformly mixed by means of a shaking machine the minimum was located near pH 6.4.

It was also found (Robbins '23, '26) that acid dyes were absorbed and retained more strongly from solutions acid to pH 6.0 and basic dyes more strongly

from solutions more alkaline than pH 6. 0. However, the absorption and retention of the basic and acid dyes overlapped somewhat; both dyes being retained to some extent between pH 4.5 and 6.0. Thus if we stain potato tuber tissue with a red acid dye, such as eosin, and a blue basic dye, such as methylene blue, the tissue is purplish. When washed with dilute buffer mixtures the methylene blue is removed almost completely in solutions acid to about pH 4.5, retained somewhat by the potato in solutions between pH 4.5 and about 6.0 and retained quite strongly by the potato in solutions more alkaline than 6.0 The eosin is lost completely in solutions alkaline to 6.0 and retained in increasing amounts by the potato in solutions acid to that point.

The potato tissue also shifts the reaction of dilute buffer mixtures toward an equilibrium point which lies near pH 6.0. This was observed first in the studies on water absorption. A complicating factor in this case was the carbon-dioxide produced by the tissue. The effect of potato tissue on the reaction of solutions was later studied specifically by placing it in the dilute buffer mixture and measuring electrometrically the pH at intervals while bubbling hydrogen through the liquid until equilibrium was reached. The hydrogen removed the carbon dioxide. Under such circumstances the equilibrium points found (Robbins and Scott'25) in some experiments ranged from pH 6.02 to 6.44.

An exact definition of this point, which, for lack of a better term, I have called the isoelectric point of the potato tuber tissues, is impossible. By all three methods its position is indicated as being in the vicinity of pH 6.0. In the first place the colorimetric method of determining the hydrogen-ion concentration is not accurate to more than 0.1 or 0.2pH. The potato tissue also changes the reaction of the solution unless the solution is strongly buffered or very large in volume as compared to the amount of potato tissue. This is a particularly disturbing factor if the tissue is allowed to stand quietly in the solutions. Under such circumstances the reaction may change materially in the vicinity of the tissue and a determination on the solution as a whole will not represent the reaction to which the potato tissue was subjected during the experiment. Finally, its position is affected by the salts used in the buffer mixtures, as is indicated by the results secured with the phosphate, citrate, and phthalate in the experiments on water absorption.

ISOELECTRIC POINTS OF OTHER PLANT TISSUES

Only a summary of the results of the determinations of the isoelectric points for other plant tissues can be given here. The isoelectric point for soybean root tips (Robbins and Scott '25) as determined by the effect of the root tips on the reaction of solutions is pH 6.2–6.44 That for *Elodea* (Robbins '26) as determined by the dye method is pH 5.8–6.2 As determined by the dye method the isoelectric point for the mycelium of *Rhizopus nigricans* is near pH 5.0 (Robbins '24). Determined by the dye method (Robbins '26) and the effect of the tissue on the reaction of solution (Robbins and Scott '25) the isoelectric point for *Fusarium oxysporum* is pH 4.9–5.0. that for *Gibberella Saubinetii* (Robbins and Scott '25, Robbins '26) is near pH 6.2 and that for *Fusarium Lycopersici* (Robbins '24,

Scott '26)is pH 5.4–5.5. Scott ('26) has made an extensive study of the effect of the mycelium of *Fusarium Lycopersici* upon the reaction of solutions. He used chiefly 0.001 M concentrations of sodium phosphate, potassium phosphate, sodium acetate, potassium phthalate, potassium chloride, calcium chloride, copper chloride, and mercuric chloride.

The highest equilibrium point reached from the acid side was pH 5.7 and the lowest from the alkaline side was pH 5.3.   The average of about 50 individual experiments was pH 5.4.

Tolerance of Potato Tissue for Hydrogen Ions and the Influence of Calcium Salts on this Tolerance

In the course of experiments on water absorption by potato tuber tissue in sodium phosphate buffer mixtures it was observed that the tissue died rapidly in solutions acid to about pH 4.5. Death was shown by a rapid loss in weight. This indicates that the acid limit for the existence of thin discs of potato tuber tissue in dilute solutions of sodium phosphate is about pH 4.5.

An unsuccessful attempt was also made to determine the alkaline limit. Four pieces of potato tuber tissue placed in 1000 cc. quantities of sodium phosphate buffer mixtures with the sodium constant at 0.01 N, of reactions pH 7.9, 8.6, 8.9, 9.4, and 9.75 remained stiff, turgid, and apparently normal for more than 30 hours.

The fact that potato tuber tissue dies rapidly in dilute sodium phosphate buffer mixtures acid to pH 4.5 is extremely interesting because the isoelectric point of the principal protein, tuberin, found in potato is close to that point (Cohn, Gross, and Johnson'20, Cohn '20, Pearsall and Ewing '24).

These results explain why Pearsall and Ewing ('24[a]) found a rapid exosmosis of chlorine from potato tuber tissue in solutions of pH 4.4 or more acid. The exosmosis which they observed was due to the death of the potato tuber tissue in these acid solutions, and one of the characteristic changes which occurs with the death of tissue is a decrease in the ability of the cells to retain certain types of dissolved material. Their results on the effect of hydrogen-ion concentration on the loss of anthocyan by beet tissue and the results of Hoagland and Davis ('25) on the loss of chlorine by *Nitella* in solutions acid to pH 4.6 are probably explainable on the same basis. It should be emphasized that such results do not present a full picture of the changes in ion movement produced by changing pH values, as might be inferred from the statements of Pearsall and Ewing ('24[a]), and are not necessarily significant from the standpoint of the absorption or loss of dissolved material by normal tissue.

By suitable experiments it was also found that calcium salts decidedly influence the effect of the acid solutions upon the potato. While the potato tissue rapidly loses water and dies in solutions of sodium phosphate which are acid to pH 4.5, it absorbs water and remains alive for some time in such solutions if a small amount of a calcium salt (0.00068M) is added.

Other investigators (Loeb'22[a]), Brenner '20, Prianischnikov '23, Port '25, Domontorich '27, Lundengardh '24) have found that calcium salts protect living tissue against the harmful effect of hydrogen ions.

I cannot explain the protective action exerted by the calcium ion against the toxic effect of hydrogen ions on potato tuber tissue. There is the possibility that the injury in acid solutions is due to the loss of essential mineral elements and the calcium prevents this loss in the way suggested by True('22) and others. The potato tissue shows a slower loss of ash elements in the acid solutions in the presence of calcium than in its abscence. However, it is impossible to say on the basis of our present information whether this loss precedes injury and death or follows it. It may be due to an effect of the calcium in retarding the diffusion of hydrogen ions into the cells, as suggested by Loeb(22ᵃ). The correlation of the killing reaction in pure sodium phosphate solutions with the isoelectric point of the tuberin, suggests, however, that calcium in some way prevents the precipitation of the tuberin, which would otherwise occur at its isoelectric point. Fenn ('16) states that when calcium chloride is added to gelatin containing hydrochloric acid the amount of alcohol needed for precipitation is increased. Lehmann ('22) found that the addition of strontium chloride, calcium chloride, or barium chloride to normal blood inhibits its coagulation in the ascending series $Sr < Ca < Ba$.

Hydrogen-Ion Concentration and the Toxicity of Cations and Anions

If the assumption that plant tissue responds much like an ampholyte is correct, we might expect to find that cations would be more toxic in solutions alkaline to the isoelectric point than in solutions acid to the isolectric point since they would be absorbed by and react with the protoplasm in greater amounts from the former solutions. This would involve the assumption that substances become toxic when they combine to too great an extent with the living constituents of the cell, a conception originated by Luchsinger in 1877 as a result of his study of the effect of alkaloids and the antagonism which he observed between the effects of two alkaloids. Anions, since they would be absorbed in greater amount from solutions acid to the isoelectric point, would evidence their injurious effect more strongly in such solutions. Complicating factors such as the effect of reactions upon the volatility, solubility, and dissociation of the toxic compound would, of course, have to be taken into consideration.

We have tested this hypothesis with potato tuber tissue (Robbins '26) and also with the spores (Scott '26) and mycelium of fungi whose isoelectric points had been determined by one or more of the three methods given above. In general, the results support the hypothesis.

In the case of potato tuber tissue the experimental procedure was as follows: A weighed quantity, approximately 10 gms. of potato tuber tissue cut into discs as previously described, was placed in 200 cc. of buffer mixtures in 600 cc. beakers to which a constant quantity of the toxic material was added. The beakers and contents were then shaken about 90 times a minute on a shaking machine.[3]

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[3] The shaking was found advisable because the reaction of the liquid in the alkaline solutions became decidedly more acid in the immediate vicinity of the potato tuber tissue when the material was allowed to stand quietly during such periods of time as were used here. This increase in acidity was due to the carbon dioxide formed by the potato and to the absorption of cations.

The shaking scarcely disturbed the position of the potato discs as they rested on the bottom of the beakers but kept the supernatant liquid thoroughly mixed. After 8 to 12 hours the potato was removed, blotted dry, weighed, and replaced in a fresh quantity of the buffer mixture. After 12 hours of further shaking the potato was again weighed and then placed in redistilled water and allowed to stand quietly for from 7 to 10 hours. The potato was removed from the buffer mixtures and placed in redistilled water for the third period in order to permit it to show its water absorptive power free from the osmotic effects of the constituents of the buffer mixture and the added substances.

Each experiment was performed in duplicate. Pyrex glassware and water redistilled from alkaline and acid permanganate were used throughout the investigation. Hydrogen-ion concentrations were determined by Gillespie's ('20) colorimetric method. Sodium chloride and the basic dyes, brilliant green (Schultz no. 428),[4] and dahlia (Schultz no. 451), were used to supply toxic cations. The acid dye, eosin (Schultz no. 512), was used to supply a toxic anion. These substances were selected because at the concentrations used they are soluble in the buffer mixtures of sodium hydroxide and phosphoric acid over the entire range of reactions employed. They also each consist of ions distinctly different in intensity of toxic action. It was manifestly inadvisable to use for this study a substance consisting of a cation and anion of approximately equal toxicity.

The injurious influence on the absorption of water by potato tuber tissue of toxic concentrations of a cation, sodium, and of certain basic dyes, dahlia and brilliant green, was more marked on the alkaline side of approximately pH 6.4, and the injurious influence of the cyanide anion and of the acid dye eosin was more marked on the acid side of pH 6.4. The results with eosin were particularly striking. A concentration (1-10,000) of this acid dye which almost completely inhibited water absorption on the acid side of the isoelectric point, at pH 5.0, had almost no effect on the alkaline side of the isoelectric point at pH 7.0. This was evident while the potato remained in the buffer mixtures containing the dye and persisted after the potato had been transferred to redistilled water. The influence of the hydrogen-ion concentration upon the toxicity of the basic dyes used was not so marked. During the period of immersion in the buffer mixtures containing the basic dyes the potato tuber tissue was affected by these dyes to much the same extent at all reactions. However, when removed from the buffer mixtures and dye to redistilled water the potato tissue which had been in the buffer mixtures alkaline to about pH 6.4 absorbed less water or lost more than that which had been in the more acid solutions. The same results were secured where uniform concentrations of sodium chloride were added to the buffer mixtures. While these results indicate that the basic dyes and the cation sodium are more injurious in solutions alkaline to the isoelectric point, their injurious effect extends also to the acid side of the proposed isoelectric point.

It was found also that concentrations of sodium chloride of from 0.054M to 0.092M caused a marked depression in water absorption in the vicinity of pH

[4] Schultz, G., and P. Julius. Organic coloring matters. (Edited by A. P. Green.) 2nd Ed. Macmillan Company, 1904.

6.0. After 21 hours in the buffer mixtures to which 0.092M sodium chloride had been added this depression amounted to 1 gm. for 10 gms. of potato tuber tissue. A surprising fact regarding this depression is the slight shift of hydrogen-ion concentration required to produce it. Thus in one experiment after 21 hours at average pH 5.95 the water absorption by 10 gms. of potato tissue was 750 mgms, at pH 6.0 the potato had lost 500 mgms., and at pH 6.55 the absorption was 500 mgms. While it is not safe, because of the error possible in the colorimetric determination of hydrogen-ion concentration, to say that the change of 0.05 pH from pH 5.95 to 6.0, caused a difference of 1.25 gms. in the water absorbed by 10 grams of potato, I can say that in the presence of a suitable quantity of NaCl a very small shift in hydrogen-ion concentration, probably not over 0.1 pH caused such an effect. A somewhat similar depression was observed in solutions of potassium cyanide.

This great change in water absorption in a narrow range of hydrogen-ion concentration is of interest in connection with a criticism made by Henderson of Fischer's colloidal theory of water absorption. Henderson pointed out that the difference in water absorption induced in colloidal material by ranges of hydrogen-ion concentration commensurate with those which are known to occur in living organisms were too small to be significant. In potato tissue, however, a slight change in hydrogen-ion concentration in the presence of a suitable quantity of sodium chloride produces an enormous change in the amount of water absorbed. Other living tissues may respond in the same way.

A considerable body of literature has accumulated which, viewed as a whole, indicates that many bases and salts with toxic cations have their toxicity increased by a decrease in hydrogen-ion concentration and many acids and salts with toxic anions have their toxicity increased by an increase in hydrogen-ion concentration. This literature has been summarized elsewhere (Robbins '26). The explanations offered for this phenomenon fall into two groups. Some consider the effect to be one on the living cells, others that it is an effect upon the acid, base, or salt. Prowazek ('10) concluded that the most probable explanation for the effect of reaction on the toxicity of alkaloids was that the typical disintegration of infusorial protoplasm produced by alkaloids was antagonized in some way by a contrary action of dilute acids. Kligler ('18) considered that the reaction of the medium modifies the specific action of the antiseptic probably due to an alteration in the bacterial cell. Stearn and Stearn ('24) explained the influence of reaction upon the bacteriostatic action of basic and acid dyes as due to the hydrogen-ion on the combination of the dye with the bacterial protein and lipoid. Bonacorsi ('00) concluded that the influence of hydrogen-ion concentration on the toxicity of substances is partly due to its effect on the degree of dissociation of the compound and partly in changing the permeability of the bacterial cell. The effect of alkalinity in increasing the toxicity of alkaloids was considered by Pribram ('11) as probably due to the fact that since alkaloids are less soluble in alkaline solutions their partitition coefficient between the living cells and the solution would be increased in favor of the former. Traube ('12, '12a) observed that the addition of sodium carbonate increased the toxicity of such substances

to tadpoles and the surface tension of cocaine, chinin, cinchonidin, aconite, atropin, phystostiginin, pilocarpin, and dionin, but had little effect on either the toxicity or surface tension of morphine and scopolamin. He therefore concluded that the increase in surface tension was causally connected with the increase in toxicity. Crane ('21), and Michaelis and Dernby ('22) explained the increase in the toxicity of alkaloids by alkalinity and the increase in the surface tension of alkaloids by alkalinity as due to the increase in the amount of the free base produced under alkaline conditions. As expressed by Crane, "in solutions of bases having dissociation constants of the order of 1×10^{-10} there is very slight variation in the proportion of free base present with the changes in hydrogen-ion concentration studied (pH 6.0–8.0) and there is very little variation in toxicity. The hydrolysis of the alkaloids with dissociation constants around 10^{-7} is definitely affected by a change of pH 6.0 to pH 8.0, as is also toxicity. The increase in proportion of free base occurs in the group of drugs with constants around 10^{-3} or 10^{-4}. Variations in hydrogen-ion concentration affect the toxicity of alkaloids by changing the proportion of free undissociated base in solution rather than by an action directly upon the cell."

I have found that the toxicity of two basic dyes, dahlia and brilliant green, and the cation, sodium, to potato tuber tissue is increased in solutions alkaline to about pH 6.4, and that the toxicity of the acid dye, eosin, and of potassium cyanide is increased in solutions acid to about pH 6.4. The effect of the hydrogen-ion concentration on the toxicity of these anions and cations is analogous to its influence on the combination of the ions with an ampholyte having an isoelectric point near pH 6.4. The position of this point agrees well with the apparent isoelectric point of potato tuber tissue as found by other methods.

This analogy may be due to the effect of the hydrogen-ion concentration on the toxic material, for example, on the amount of free base or free acid formed and not to the fact that potato tuber tissue acts like an ampholyte with an isoelectric point near pH 6.4.

With the exception of brilliant green the dissociation constants of the substances used in this investigation could not be found in the literature. For brilliant green, according to Scudder ('14), $kb \times 10^3$ is less than 5.3. Calculating the free base present by the formula

$$p = 1 + \cfrac{1}{\cfrac{Kb\ H}{Kw}}$$

we have the following values: at pH 3, 1.88×10^{-8}; pH 5, 1.88×10^{-7}; pH 6, 1.88×10^{-6}; pH 7, 1.88×10^{-5}; pH 8, 1.88×10^{-4}; pH 9, 1.88×10^{-3}; pH 10, 1.85×10^{-2}; pH 11, 1.6×10^{-1}; pH 12, 6.53×10^{-1}; pH 13, 9.5×10^{-1}. From pH 3 to 10 the amount of free base increases almost uniformly 10 times for each Sörensen unit, the amount of increase becoming slightly less as pH 10 is approached. The sudden increase in toxicity of 1 : 2,500,000 brilliant green in solutions alkaline to about pH 6.0 could not, therefore, be accounted for on the assumption that it is due to the effect of the free base formed unless it happened that the amount of free base

present at pH 5.5 was not sufficient to be toxic and the 10 fold increase at pH 6.5 resulted in sufficient to be toxic. If such an explanation of the results secured with brilliant green is correct then it would be an unusual coincidence that sodium chloride and dahlia should be affected in the same way and that the amount of free acid formed from the acid dye eosin and from potassium cyanide should be relatively non-toxic at pH 6.5 and become toxic at 5.5.

Two methods might be suggested of determining more definitely whether the influence of hydrogen-ion concentration upon the toxicity of cations and anions is due to its effect upon the formation of free base or free acid upon the combination of the toxic ions with the constituents of the protoplasm. We might use toxic materials with distinctly different dissociation constants. We might use organisms which appear to have distinctly different isoelectric points.

Miss Kobs has used the latter method. She made use of three fungi—*Rhizopus nigricans*, *Fusarium oxysporum*, and *Gibberella Saubinetii*. The isoelectric points for the first two organisms had been determined to be near pH 5.0 and for the third near pH 6.2. The three fungi were grown on nutrient agar or in solution cultures, the reactions of which were adjusted with phosphoric acid or sodium hydroxide so as to yield a series of reactions from about pH 3.5 to above pH 8.0. To the media uniform toxic concentrations of the acid dyes, eosin or rose bengal, or of the basic dye, dahlia, were added. For *Rhizopus nigricans* the toxicity of the acid dyes was decidedly increased in media acid to about pH 5.0 while that of the basic dye was markedly increased in media of reactions alkaline to pH 5.0. The critical point for *Gibberella Saubinetii* was near pH 6.0. The influence of the reaction upon the toxicity of the dyes for *Fusarium oxysporum* was not so marked. The critical point appeared to be near pH 6.0. For two of these three fungi the influence of hydrogen-ion concentration on the toxicity of the acid and basic dyes used is correlated with their isoelectric points.

Scott ('26) found the influence of hydrogen-ion concentration upon the toxicity of mercuric chloride, the basic dye, methylene blue, and the acid dye, eosin, for the germination of the spores of *Fusarium Lycopersici* to be correlated with the isoelectric point of that fungus.

We have also found *Elodea* (Robbins '26) to respond to toxic concentrations of acid and basic dyes at different hydrogen-ion concentrations with pH 5.8 to 6.2 as the critical point.

These results indicate that an important factor in the influence of hydrogen-ion concentration upon the toxicity of cations and anions is due to its effect upon the combination of the ions with the plant tissue and that in this combination the plant tissue responds much as an amphoteric colloid, such as a protein, does.

The results emphasize the importance of considering hydrogen-ion concentration in the investigation of the toxicity of other substances and the importance of considering the effect of other ions in studying the influence of the H or OH ions. upon living tissues. It is evident that the kind and concentration of anions may have a decided influences on the acid tolerance of an organism and that the presence of toxic concentrations of cations will affect the alkaline tolerance. In the presence of certain toxic concentrations of both cations and anions the hydrogen-

ion range for an organism should be narrowed. Solutions of organic acids, which have long been known to be more toxic than their hydrogen-ion concentrations would indicate, owe their toxicity to the organic anion which they contain and the effect of acidity in favoring the combination of this organic anion with the protoplasm. Evidently the ideal disinfectant would be one with both a toxic anion and cation (mercurochrome) for such a compound would be injurious on both the alkaline and acid side of the isoelectric point.

The Isoelectric Point, Growth, Spore and Seed Germination, and Infection by Fungi

If plant tissue responds like a protein with an isoelectric point within the range of hydrogen-ion concentrations compatible with life, we might expect growth and the germination of spores and seeds to show a bimodal curve under the influence of hydrogen-ion concentration with the minimum between the two maxima located at or near the isoelectric point. This conclusion follows from the fact that water absorption and consequently the turgor is reduced at the isoelectric point. The reduction in turgor would result in a decreased growth and a reduction in or slowing up of spore germination and seed germination in the vicinity of the isoelectric point. The presence of injurious concentrations of cations would result in the elimination of one of the two maxima and the production of a monomodal curve with the optimum on the acid side of the isoelectric point. In the presence of injurious concentrations of anions a monomodal curve would be produced with the maximum on the alkaline side of the isoelectric point.

A considerable number of observations have accumulated (Robbins '23) which show that when plant growth or the germination of seeds or spores is plotted against the hydrogen-ion concentration of the substrate a bimodal curve is frequently produced. Hopkins ('21, '22) in this laboratory found this to be true for the germination of the spores of a strain of *Gibberella Saubinetii*, also for the growth of this organism and for the germination of wheat grains. Scott ('24) found it to be true for the growth of *Fusarium Lycopersici* and for the germination of the spores of the same fungus. The minimum between the two maxima was correlated with the isoelectric point for *Fusarium Lycopersici*, pH 5.4–5.5, as determined by the dye method and by the effect of its mycelium upon the reaction of solution in which it was immersed. In addition, the isoelectric point of the mycelium of *Rhizopus nigricans* determined by the dye method was found (Robbins '24) to be correlated with a minimum between two maxima when the fungus was grown on media of varying hydrogen-ion concentration.

It also seems probable that the isoelectric point is correlated with the ability of certain fungi to infect their host plants. The infection of plants by fungi which enter through the unpierced epidermis is due in some cases to a pressure process. A minimum water absorption would mean a minimum pressure and a minimum infection. We might expect therefore the percentage of infection of plants by certain fungi in media of different hydrogen-ion concentrations to show a bimodal curve with the minimum between the two maxima at or near the isoelectric point of the fungus. Hopkins ('22) found a double maximum curve for seedling infection

of wheat by a strain of *Gibberella Saubinetii* in soils of different hydrogen-ion concentration. Scott ('24) found the same for the infection of tomato by *Fusarium Lycopersici* and in this case the minimum between the two maxima was near the isoelectric point of the fungus mycelium.

Hydrogen-Ion Concentration and the Staining of Sections of Plant Tissue

The conception of the cell as an ampholyte is of great significance in the staining of tissues. Naylor ('26) found that sections of root tips of hyacinth, buckwheat, pea, soybean, and lupine responded to acid and basic dyes under varying hydrogen-ion concentration much as a protein does with an isoelectric point lying between pH 4.6 and pH 5.0. In solutions acid to this range the acid dyes were absorbed and retained. In solutions alkaline to this range the basic dyes were retained. The parts of the cell behaved differently toward acid and basic dyes under different hydrogen-ion concentrations. The cytoplasm responded as though it had a more acid isoelectric point than the nucleus. By staining the sections with an acid and basic dye of contrasting colors and washing with dilute buffer mixtures of pH 4.6–5.0 differences in the retention of the dyes by different parts of the cell resulted in differential staining. It is generally stated that the nucleus is basophil and the cytoplasm is acidophil. By controlling the reaction of the solutions used in washing after staining, the cytoplasm or nucleus can be stained with either acid or basic dyes. The control of the reaction of staining solutions and of washing solutions offers a new approach for the differentiation of tissues and of cell parts and a new method of securing information regarding their constitution. Many applications of these principles will suggest themselves. Stearn and Stearn ('24) have already thrown much light on the nature of the Gram stain for bacteria. The probable significance of these principles in connection with the staining of the eosinophil, neutrophil, and basophil white blood corpuscles is obvious. They can probably be applied to the differential staining of parasitic organisms in host tissues. Certainly no one interested in the use of stains for either plant or animal tissue can afford to be unacquainted with the effect of hydrogen-ion concentration upon the uptake and retention of basic and acid dyes by amphoteric compounds.

I do not wish to give the impression that plant tissue is a single protein. From the evidence at hand I conclude that it acts like one protein in many ways, though not in all. Thus *Elodea*, which responds in dye absorption and in the effect of hydrogen-ion concentration on the toxicity of acid and basic dyes like an ampholyte with an isoelectric point of pH 5.8–6.2, does not affect the reaction of dilute sodium phosphate buffer mixtures as would be expected. Placed in 0.006N sodium phosphate solutions *Elodea* (Robbins '26) changed the reactions of those more acid than pH 6.5 toward greater alkalinity but did not affect the reaction of those solutions more alkaline than pH 6.5.

Fusarium oxysporum, which by its effect upon the reaction of solutions and its uptake of basic and acid dyes has an apparent isoelectric point of near pH 5.0, responded in the effect of hydrogen-ion concentration upon the toxicity of the

acid and basic dyes like *Gibberella Saubinetii* the isoelectric point of which is pH 6.2.

For potato tissue the absorption of cations and the effect of cations extend to the acid side of the proposed isoelectric point while the absorption of and effect of anions is less evident on the alkaline side of the isoelectric point. Ash determinations on potato tuber tissue which had been immersed in dilute buffer mixtures were expected to show when plotted against the hydrogen-ion concentrations of the solutions a double maximum curve with a minimum near pH 6.0. They show no minimum at the apparent isoelectric point. There was little loss of ash in solutions of pH 7.0 to 8.0, some loss in solutions of from pH 6.0 to 7.0, more loss in solutions of from pH 4.5 to 6.0 and rapid loss in solutions more acid than pH 4.5.

The results for potato tuber might be approximated by a diagram (Fig. 1) which is not intended to be a complete nor quantitative representation of the
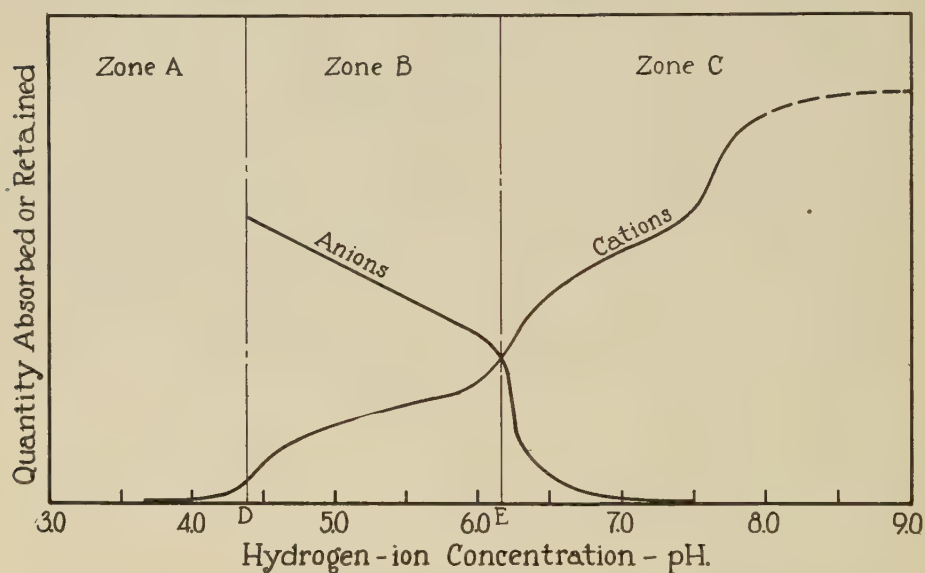
Fig. 1. A diagram of the effect of the hydrogen-ion concentration upon the absorption of anions and cations by potato tuber tissue. For the significance of the letters and zones see main body of text.

facts. The relative absorption of anions and cations in dilute sodium phosphate buffer mixtures is plotted against the reaction of the external solution expressed as pH.

At D (pH 4.3–4.5) is the isoelectric point of tuberin. At E (approximately pH 6.0–6.4) is the apparent isoelectric point of potato tuber tissue. In zone A, acid to pH 4.3–4.5, cations are not absorbed and retained, acid dyes are absorbed and retained strongly, and the potato tissue dies comparatively rapidly in dilute sodium phosphate. In zone B, between about pH 4.5 and 6.4 anions are absorbed

and retained strongly, cations less strongly, anions are especially toxic and cations are less toxic. The potato tuber tissue shifts the reaction of solutions in which it is immersed in zone A and B toward E. In zone C, alkaline to pH 6.0–6.4, the anions are absorbed and retained slightly, cations are absorbed and retained strongly, cations are especially toxic, anions much less so. There is probably a break in the cation absorption curve somewhere between pH 7.0 and 8.0. In zone C, the potato tissue shifts the reaction of solutions in which it is immersed toward E.

The differences which exist between the response of a pure protein and that of plant tissues to hydrogen-ion concentration may be due to the presence of a mixture of proteins rather than a single one, to the presence of proteins and non-proteinaceous colloidal material, or it may be due to salt formation. The hydrogen-ion concentration for minimum dissociation when proteins form true salts may coincide with the isoelectric point or may lie on either side of it, depending upon the dissociation constants of the salts formed. Nevertheless, assuming plant tissue to respond much like an amphoteric compound with an isoelectric point within the range of reactions compatible with life is a useful hypothesis, and considering plant tissue as an amphoteric colloid which reacts with ions according to chemical laws rather than as osmotic chambers with membranes of changeable permeability is a possibility which we cannot afford to neglect.

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THE PERMEABILITY OF PLANT INTEGUMENTS FOR IONS[1]

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Seventy years ago Du Bois-Reymond started the investigations on the electric potential differences in muscles and nerves, the resting, injury, and action currents. A huge number of facts in this field of physiological experimentation both in zoological and botanical material have been accumulated since that time. However, the physical meaning of all these discoveries could not be understood before a very important observation was made—not only made but also consciously recognized as an important observation. Probably even the first investigators in this field occasionally did make the observation that the magnitude of the potential differences (P.D.) between two places of some physiological material depends on the composition of the solutions by means of which this potential is led off to the unpolarizable electrodes, but this fact obviously aroused only a secondary interest. Later on, different observers stated the influence of the connecting liquid. Oker Bloom showed that the P.D. is very different when the connecting liquid is pure water and when it is a physiological salt solution. However, we cannot see a systematic principle in the early investigations on this subject, as the development of the physical chemistry of solutions of electrolytes had not then reached a degree sufficient for that purpose. As a decisive step for a long time, let us go on directly to a series of experiments which in my opinion are apt to lead us the right way, and which may be represented to you not literally in the original manner of those authors, but so as to give you a connecting link with what is to follow in this paper.

In 1912 J. Loeb and Beutner described the following observations: When two equal solutions of any electrode are in contact with an apple, the one solution touching the intact peel, the other dipped into a perforation of the apple peel and touching the sap of the pulp, a potential difference is established which can be measured with a good degree of accuracy. It varies with the individual apples. When we perform a series of experiments with one apple, it varies also with the concentration and kind of the dissolved electrolyte of that solution which is in contact with the intact peel, but it does not vary to an appreciable degree with the composition of that solution which is dipped into the pulp. It is quite obvious that the potential difference between the sap of the apple and that liquid which is connected through the perforation is of no appreciable interest, while all interest should be concentrated upon that potential difference which is established between the sap and that liquid which is separated from the sap by the intact peel.

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When the contact 0 (in Fig. 1, A) remains unchanged in a series of experiments and the solution 1 is varied, the E.M.F. of the different chains obtained in this way differ from each other. This difference depends upon both the concentration and the kind of the electrolyte dissolved in liquid 1.

We may also establish a chain directly between two places of the intact peel without any perforation (Fig. 1, B). One solution (No. 1) is in contact with, let us say, a solution of $N/10$ K Cl, the other solution is represented by a drop of, let us say, $N/100$ K Cl (No. 2) which is placed upon a suitable spot of the
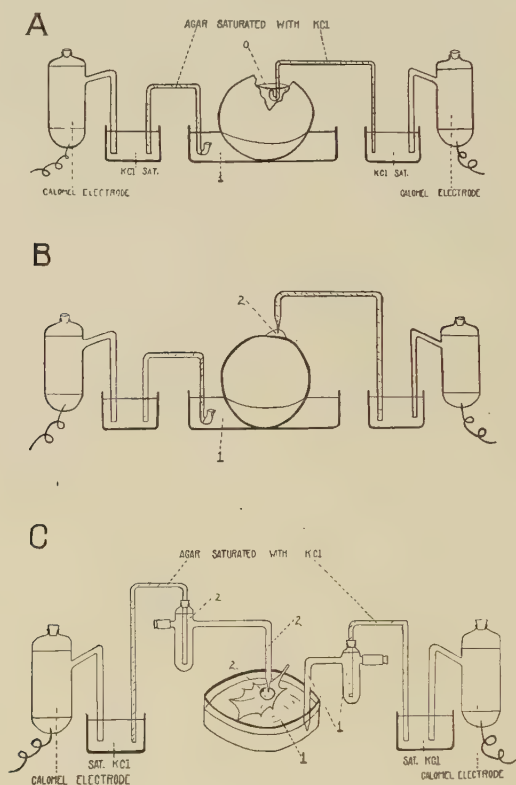
Fig. 1.

apple so as not to run down. The P.D. of such a chain has turned out to be almost accurately the difference of the E.M.F. of the following two chains. First measure the E.M.F. of a chain of the first type, with any arbitrary solution at place O, and a solution of $N/10$ K Cl at place 1; and after that the E.M.F. of a similar chain, in which an $N/100$ solution of K Cl has been substituted for the $N/10$ solution at place 1. The difference between the E.M.F. of these two chains is equal to the P.D. of the chain of the other type. In an apple, the first method is easier, only on account of technical considerations. In other cases, the second type is easier. Fig. 1, C shows how a chain of the second type can be made up very easily when we apply this method to a leaf of any plant. The one liquid is

beneath the leaf, the leaf floating on it. The other liquid forms a drop on the upper side of the leaf. Again, either solution may be present in the form of a drop, the two drops on the same side of the leaf, but so as not to flow together. The results of the P.D. obtained do not actually depend on whether the one or the other arrangement is used.

TABLE 1. POTENTIAL DIFFERENCES IN APPLE PEEL BETWEEN A PLACE OF INJURY IN CONTACT WITH N/10 KCl AND AN INTACT PLACE IN CONTACT WITH KCl SOLUTIONS OF THE FOLLOWING CONCENTRATIONS

		Difference
N/10	49.2 millivolts	
		>——— 21.1 millivolts
N/50	70.3 millivolts	
		>——→ 38.0 millivolts
N/250	108.3 millivolts	
		>—·—→ 40.0 millivolts
N/1250	146.0 millivolts	
Theoretical maximal difference........		40.0 millivolts

Let us now consider the results of the measurement of such potential differences. This P.D. has turned out to depend on both the concentration and the kind of the electrolyte dissolved in the solution which is in contact with the intact membrane. We may begin with the influence of the concentration. To start with the simplest case, an electrolyte consisting of a univalent cation and a univalent anion, such as NaCl or KCl, the potential of a more dilute solution compared with the potential of the intact skin is always more positive than the one of a more concentrated solution. This is the first fundamental law. The maximum value, when the proportion of the concentrations is 1:10, is 57 millivolts at room temperature and increases in an arithmetical progression when the concentration varies in a geometrical progression, for example, the P.D., when the proportion of concentration is 1:100, may reach up to 114 mv., and, when the proportion of concentration is 1:5, it is up to 40 mv. The maximum is reached only in some cases, often the P.D. is more or less lower, down to one half and even less. That depends in the first place on the kind of peel. One of the best and easiest objects, is the peel of an apple, provided it is quite intact. Any defective spot of the peel works as a leak, diminishing the effect. Similar effects sometimes as high, sometimes more or less lower, may be found in other surfaces of any part of a plant, in a stem, a leaf, a petal, etc., also in marine algae. I recommend a leaf of *Plantago*. This effect is partially diminished, but not at all completely destroyed by a previous heating of the plant in boiling water, or by a preliminary treatment with alcohol, ether, formaldehyde, mercuric chloride, and other chemicals poisonous for living cells. So this effect does not depend on the living condition of the cells.

All of that holds not only for salts of univalent cations and anions, but also for any salt consisting of a univalent cation and *any* anion, even a polyvalent one, such as sulfate, or ferrocyanide, ferricyanide, and any anion whatever. The anion has no influence at all, at least in those cases where approximately the maximum

effect is reached. Using a salt with a bivalent cation such as Ca, Ba, Sr, Mg, the maximum effect obtained is rather accurately one half of the above mentioned effect.

The maximum effect is reached, even in the best cases, when neither of the salt solutions which is compared has too high a concentration, that is, when even the more concentrated solution does not exceed, let me say, 0.1 normal. In higher ranges of concentrations the effect becomes smaller in any case and finally approaches more or less the value obtainable when the two solutions are in free contact with each other without a membrane; in fact, two different solutions, in general, produce a potential difference when they are in direct contact with each other, depending on the different mobilities of the different ions. This P.D. may sometimes even show a sign opposite to the one obtained when the membrane is interposed. I am describing only the very simple case of chains with K Cl in different concentrations; where the concentration effect is always zero when no membrane is present.

TABLE 2. POTENTIAL DIFFERENCES BETWEEN AN INJURED PLACE OF THE APPLE IN CONTACT WITH N/10 KCl AND AN INTACT PLACE OF THE PEEL IN CONTACT WITH N/10 SOLUTIONS OF THE FOLLOWING ELECTROLYTES

Electrolyte	Difference	Electrolyte	Difference
HCl	−4.8 millivolts	KCl	+20.4 millivolts
RbCl	+15.2 millivolts	KBr	+17.4 millivolts
KCl	+20.4 millivolts	KI	+18.3 millivolts
NaCl	+30.0 millivolts	K_2SO_4	+20.4 millivolts
LiCl	+36.0 millivolts	KOH	+21.1 millivolts
$CaCl_2$	+42.1 millivolts	$K_3Fe(CN)_6$	+21.2 millivolts
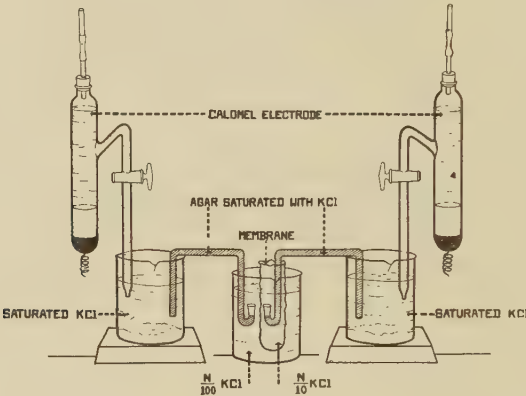
Fig. 2.

Furthermore, two solutions of salts with different cations, though in equal concentrations, show a P.D.; for example, a Na salt solution is always more positive in contact with a membrane than a K solution. The series of the different cations in ascending order of positivity is:

$$H \rightarrow Rb \rightarrow \begin{cases} K \rightarrow Na \rightarrow Li \\ NH_4 \end{cases}$$
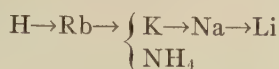
only to mention the univalent cations, because in the interpretation of the behavior of the bivalent cations there is a certain difficulty which has no particular interest and may be neglected for the purpose of the present paper.

TABLE 3.

Electrolyte	Difference	Electrolyte	Difference
HCl	54.8 millivolts	K_2CO_3	48 millivolts
KCl	47 millivolts	K_2CO_4	48 millivolts
KI	48 millivolts	$K_3Fe(CN)_6$	49 millivolts
KBr	47 millivolts	LiCl	45 millivolts
KNO_3	45 millivolts	RbCl	49 millivolts
K_2SO_4	44 millivolts	$(NH)_4Cl$	47 millivolts

So much for the facts which have been described chiefly by Jacques Loeb and the extended investigations of Beutner. Now two questions should be asked; in the first place: What is the mechanism of this effect? In the second place: Have these phenomena anything to do with those effects which are exerted by the real membranes of living cells? In the connection last mentioned I do not mean the cellulose membrane,—but the plasma membrane with its particular selective permeability, about which I need not go into detail before this audience.

In their first paper J. Loeb and Beutner assumed a different permeability of these peels for cations and anions in order to explain these effects. Later on Beutner in his own continuation of this work suggested another theory. He succeeded in imitating certain artifical systems in which a similar effect can be observed and ascribed the same mechanism which he proved bo be valid for his model, to the vegetable peels, too. This model is as follows:

When an aqueous solution is in contact with an organic solvent not miscible with water, in general an electric potential difference on the two sides of the interface will be established. It can be shown by thermodynamic consideration, at least for dilute solutions, that this P.D. does not depend on the concentration of the electrolyte, at least when the electrolyte consists of two univalent ions, if the water-insoluble phase is represented by a chemically indifferent substance such as, for example, amyl alcohol, which possesses neither the properties of a base nor of an acid. When two solutions of one electrolyte in different concentrations are separated by an intermediary layer of such a chemically indifferent oil, the two P.D's. at the two interphases are equal and of opposite direction. They cancel each other, and the E.M.F. of a chain made up in this way is zero. Certain circumstances may cause it to be not quite exactly equal to zero; these conditions are the diffusion potential within the oil and the fact that the activities of ions do not accurately correspond to their concentrations. As, however, these deviations are of no particular interest and can only bring about P.Ds.' of some millivolts, we may omit the detailed discussion of this item and maintain the above stated assertion with a certain restriction. In any case: a membrane formed by an

organic, indifferent oil such as amyl alcohol, or even pure neutral fat, is no model for the P.D. which can be found between two salt solutions of different concentration separated by a membrane such as the apple peel or the surface layer of a leaf.

If, however, such an oil has the properties of an acid or a base, or if, at least, an indifferent oil contains a small amount of some dissolved acid or base which is practially insoluble in the aqueous phase, sometimes the oil behaves like the apple skin, producing a P.D. between two solutions of different concentrations which under the same conditions reaches the maximum effect mentioned before, just as the apple skin does. To mention only one example of such an oil, there is salicylic aldehyde containing a trace of salicylic acid. Here we have a model for the behavior of the plant skins, and this is a discovery made by Beutner. This most interesting finding was one of the incentives for the newer period of the investigation in this field. The explanation of the efficiency of the presence of a small amount of an acid in the oil is rather difficult. The premise on which Beutner postulates his explanation is that such an acid as salicylic acid and others, when dissolved in the oil phase, behaves as a so-called strong acid, while it is known that these acids when dissolved in water behave as relatively weak acids, not at all comparable with H Cl, for example, which is one of the strong acids. The suggestion that a weak acid should behave as a strong acid in an organic solvent is rather surprising and is not in too good an agreement with our knowledge of the dissociating power of organic solvents. In any case, this problem requires renewed investigation. If we take this supposition as true, it can be shown, indeed, that the observed effect is a necessary thermodynamical consequence which Hoeber first inferred for the theory of the so-called glass chain. Beutner took this supposition as a basis and tried to show his effect to be a special case of the theory of potential differences at interphases according to Hoeber. However, some years later on, Hoeber and Mond found different models which produce more or less similar effects but cannot be explained at all by this theory. Hoeber showed that under certain circumstances a membrane of gelatine, casein, euglobulin, and proteins in general may represent quite good models for the same effect. These membranes cannot be considered as equivalent to the homogeneous phase of an oil, not even to any homogeneous phase whatsoever, Hoeber attributed this effect to some capillary phenomenon, since it is known, for example, that a gelatine jelly may be regarded as a system of capillaries. He did not try to go into further details in respect to this suggestion.

Now I should like to show you one more model for this effect which seems to me to be a very general one and to fit fairly well with all that we can observe in the plant peels.

When a sheet of filter paper is impregnated with molten paraffine the paraffine, after the solidification, forms a membrane which is water proof indeed but permeable for dissolved molecules in solutions. It is permeable, for example, for NaCl, sugar, and other substances. As these substances are not soluble at all in paraffine it is obvious that the permeability is due to very fine ultramicroscopic pores in the membrane. Such a membrane is like a sieve. Now, when, for instance, a 0.1 normal solution of KCl and a 0.01 normal solution of KCl are

separated by such a membrane, the more dilute solution is electropositive against the other by about 13 millivolts. Other membranes of similar properties can be made of wax, mastic, rubber, and parchment paper, all of which show the same phenomenon. The potential difference is greater or smaller, but never exceeds the above mentioned maximum value of 57 millivolts. Among such membranes the most effective one, and one which shows almost perfectly the maximum value, when prepared in a certain way, is a special kind of collodion membrane. It differs from the well known collodion membrane commonly used for dialysis in that the collodion film is completely dried and must no longer contain any trace of ether or alcohol before it is wetted with water. Such a membrane has a very poor permeability indeed compared with the usual collodion membrane, but the permeability can nevertheless be very well studied. What can be shown with greatest ease is the P.D. between two different electrolyte solutions which are separated by such a membrane. Figure 2 shows the method of measuring such a P.D. It is the same method that I previously demonstrated for plant skins. Table 4 shows the results. The idea is evident, namely, that the effect of such a

TABLE 4.

Solutions used	Difference
HCl	-93 millivolts
RbCl	-8 millivolts
$(NH)_4Cl$	-6 millivolts
KCl	0 millivolts
NaCl	$+48$ millivolts
LiCl	$+74$ millivolts

membrane is also due to a sieve structure. An interpretation of the P.D. can be made by the assumption that the cations go through the pores of the sieve with a higher speed than the anions. It follows from the theory of the liquid junction potentials that the maximum effect which I mentioned several times is reached when the anion cannot diffuse across the membrane at all. This assumption was corroborated by diffusion experiments. For instance, when solutions of KNO_3 and NaCl ions are separated by such a membrane, K and Na ions are slowly but obviously exchanged through the membrane, while the Cl does not diffuse in an appreciable amount, even in many days. One can see from such an experiment that practically the cations alone may move through the pores of the membranes. When a solution of KCl is separated from pure water by such a membrane, neither K nor Cl penetrates the membrane. The K ions, though movable by themselves, are prevented from diffusion by the electrostatic attraction of the immovable Cl ions. Such diffusion experiments show that the interpretation of the P.D. was justified and we may use this easier method of measuring the P.D., to study the mobilities of the different ions in the membrane. I can here give only the definite results. These are shown in Table 5. The mobilities of different ions differ in a simple aqueous solution also. But the difference is largely increased, I should say exaggerated, in the membrane. The anions are

TABLE 5. RELATIVE MOBILITIES OF CATIONS

	Li^+	Na^+	K^+	Rb^+	H^+	Ratio Li:H
Relative mobility in a simple aqueous solution	0.52	0.65	1.00	1.04	4.9	1:9.4
Relative mobility within the dried collodion membrane	0.048	0.14	1.0	2.8	42.5	1:890

not movable to any appreciable extent. The potential differences are of the same character as in the apple skin. We ought to investigate, therefore, the diffusibility of the different ions in the apple skin also by diffusion experiments. Table 6 shows the result.

TABLE 6. DIFFUSION OF POTASSIUM FROM THE APPLE SAP THROUGH THE INTACT PEEL WHEN THE APPLE IS DIPPED INTO N/10 NaCl, OR PURE H_2O

Time	N/10 NaCl	pure H_2O
After 1 day	0	0
After 3 days	trace	0
After 5 days	0.01 mg K (?)	0
After 7 days	0.03	0
After 11 days	0.12	trace (??)
After 17 days	0.16	0.004 mg (?)

It is obvious that when the apple is dipped into pure water the K, which is present in large amount in the apple sap, does not come out, not even in two to three weeks. But, when it is dipped into a solution of NaCl, K can be detected in the outside solution, increasing from day to day. Thus the dried collodion membrane is a nearly perfect model of the surface skin of a leaf or an apple. There remains to be explained the mechanism of this effect. The assumptions necessary for this explanation are not quite new, having been used already in the study of electroendosmosis, and especially in some other investigations made by Bethe and Toropoff on membranes. All of the membranes mentioned have the common property of being electronegative against water and most of the aqueous electrolyte solutions, a fact easily proven by the direction of the water current in electroendosmosis. Now, a negative charge of a solid substance in contact with a solution means that this substance adsorbs negative ions from the solution. It does not matter whether this process of adsorption is a physical or chemical combination, and we may avoid the discussion of the forces which bring about this adsorption. The consequences do not depend upon the nature of these forces. In any case, adsorption of negative ions means that the adsorbed ions have lost their freedom of motion. Only those anions within the pores, or channels within the membrane, which are not adsorbed can move. When there is a difference in the concentration of a given ion on both sides of the membrane a diffusion takes place, the velocity of which depends on the difference in concentration and on the frictional resistance. This friction is almost infinitely increased for the ad-

sorbed anions. When the concentration of the electrolyte is small, practically all of the anions within the channels of the membrane may be adsorbed. In this case the maximum effect of the potential difference is reached, as may be shown by a simple calculation, with which any physical chemist is familiar. In higher concentrations, according to the general law, the adsorption will not be complete. Then we have both movable and immovable anions, and there will be a certain average mobility of the anions which is smaller than the usual one. So we obtain potential differences which do not quite reach the possible maximum value. If it were possible to work with membranes with a positive charge, the cations, instead of the anions, should be retarded in diffusion, and the sign of the potential difference should be reversed. This was confirmed in part by Mond, in Hoeber's laboratory, and by Fujita, in my laboratory, for membranes such as gelatine and other amphoteric membranes. These show the normal effect when they are negative, that is, when they are in contact with a solution of a pH greater than the isoelectric point of the gelatine, but they show a reversion of the potential difference when they are in solution of an acidity high enough to charge the membrane positively.

What I have said about the large differences among the cations in respect to their mobilities in a dried collodion membrane may be easily understood if we think of the different degrees of hydration of the ions. Every ion drags along a shell of water molecules, the amount of which increases in the series, for example, $Rb < K < Na < Li$. The difference in the amount of water dragged along in diffusion is responsible for the difference in the mobilities of these ions in general. Now, the frictional resistance exerted against the movement of this water shell is increased when the water shell is wedged in the pore, the wall of which is wetted by water. The greater the water shell the stronger is it wedged in the channel, and an additional friction against the motion of the ion arises, which depends on the degree of hydration of the ion in a much higher degree than the friction in the usual aqueous solution. In this way the remarkable result is brought about that a membrane with very narrow pores, for example, may be considered as practically impermeable for Na in comparison with K, and again, practically impermeable for Li in comparison with Na, and again, as practically impermeable for any anion in comparison with Li. So we begin to understand in how far specific permeabilities may depend on physical properties of the membrane, especially on the size of pores and the electrical charge. Now the question arises as to whether this kind of membrane has anything to do with the plasma-membrane proper, which is of much greater biological importance, and whether a similar mechanism may be found in the plasma-membrane and may be supposed to be responsible for the different kinds of selective permeabilities of the plasma-membrane of living cells. The difference between the collodion membrane and the apple skin, on the one hand, and the plasma-membrane on the other, seems to me to consist in the following: The collodion membrane, the paraffine membrane, and others, such as the apple skin, are relatively resistant solid membranes with a definitive ultramicroscopical sieve structure which practically cannot be influenced by the nature of the surrounding liquid and the electrolyte content of

this liquid, provided, of course, that the liquid is, for example, not just a solvent for collodion, such as ether. The bivalent ions, especially such as Ca, do not influence the structure of these membranes. The plasma-membrane, on the other hand may be interpreted as in the image of a sieve also, but the structure of this sieve can be altered by the surrounding liquid. The substance of the plasma-membrane is justly assumed to be some kind of a lipoid, but not such a resistant stubborn lipoid as the wax-like substance of the apple skin or the solid and rigid collodion, but a weak lipoid, which, perhaps in combination with proteins, is in a colloidal condition and in a certain degree of dispersion, which stands midway between a sol and a coagulated colloid. It is well known how much the degree of dispersion or flocculation can be influenced by electrolytes, and particularly by bivalent ions such as Ca.

Now, when the colloidal state and hence also the structure and the pore-size of a membrane depends on the surrounding solution, the electrolyte content of this surrounding solution has a double influence. In the first place, it determines the structure of the membrane, the size and shape of the pores, and the electric charge. Particularly the bivalent ions, such as calcium, will be of great influence in this respect. Clowes has even shown that the presence or the absence of calcium is the deciding factor whether an oil and water system consists of a dispersion of oil drops in water or of water drops in oil. This influence of the electrolytes, of course, has nothing to do with such membranes as the cuticle of an apple or of a leaf, with their skin like an elephant's. But, the temporary structure of the more sensitive plasma-membrane under the influence of the surrounding liquid being given, we may try to study the permeability of the different ions through this membrane in the same way as we did in the case of the other membranes. So we may split the problem of the permeability of the plasma-membranes into two separate problems. In the first place, there is the influence of the surrounding solution on the structure and other physical conditions of the membrane. To this problem the present paper does not make any contribution. In the second place, there is the physical mechanism of the selective permeability in a membrane of a given structure. It should be expected that in the continuation of these investigations there would be an attempt to find out in how far the described facts and their interpretation might be applied to this problem also.

DER EINFLUSS DER RADIOAKTIVITÄT AUF DEN PFLANZENORGANISMUS[1]

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Mit unseren Forschungen, die wir bereits im Jahre 1906 begonnen haben, stellten wir uns die Aufgabe, die physiologische Wirkung der einzelnen Radium-strahlen auf die gesamten Kraft- und Stoffwechselprozesse der Pflanze zu er-gründen.

Ich verwendete zu diesem Zwecke verbesserte und modifizierte Apparate von Bonnier, und Mangin, sowie von Willstätter, und durch zahlreiche mit meinen Mitarbeitern ausgeführte Experimente überzeugte ich mich, dass man durch Anwendung schwacher Aktivität die Assimilations- und Dissimilationsprozesse exakt verfolgen kann.

Der Radioaktivität ist beim Atmungsprozesse des pflanzlichen Organismus eine wichtige Funktion zugewiesen. Der primäre Vorgang der Atmung ist stets eine intrazellulare Atmung und es sind dies die Reduktionsprozesse, die durch die Radioaktivität und zwar durch die Beta-Strahlen unterstützt werden. Die Radioaktivität gibt den Anstoss zur Umlagerung der Atome in den grossen Molekülen des Zuckers und es bildet sich zuerst Milchsäure, aus der Milchsäure entsteht Kohlensäure und Alkohol und weiter Acetaldehyd und Essigsäure. Die Mechanik der Umlagerung der Atome in den Molekülen wird durch die Pflanzenzymase und Pflanzenlaktazidase hervorgerufen. Durch unsere jetzigen, im grossen Masstabe ausgeführten Versuche, sind unsere alten Befunde neuer-lich bestätigt worden, dass nämlich der primäre Prozess der Atmung eine neue Art der alkoholischen Gärung ist. Erst durch die von der Oxydase und Peroxy-dase hervergerufenen Oxydationsprozesse, die von den Alfa-Strahlen des Radiums gefördert worden, bilden sich Oxydationsprodukte, die sich dann zuletzt in Kohlensäure und Wasserstoff spalten.

Sehr interessante Resultate erzielten wir mit der Radiumemanation. In Gegenwart von Radiumemanation, bei voller Abwesenheit von Sauerstoff findet man, dass sich der Alkohol bei der intrazellularen Atmung oxydiert und in Azetaldehyd, Essigsäure und Kohlendioxyd verwandelt wird. Die Radium-emanation, resp. die Alfa-Strahlen sind in der Natur ungemein verbreitet. Durch die Tatsache, dass alle Bodenarten mehr oder weniger radioaktive Stoffe enthalten und infolgedessen die Emanation aus dem Boden in die Luft aussenden, ist die Luft stets mehr oder weniger radioaktiv. Alle Pflanzen sind sehr schwach rakioaktiv und durch unsere jetzigen vertieften Kenntnisse über die Verbreitung

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und Wirkung der Radioaktivität öffnen sich uns ganz neue Perspektiven über das Leben der chlorophyllosen und chlorophyllhaltigen Zelle.

Durch unsere Versuche konstatierten wir tatsächlich, dass durch die Einwirkung der Alfa-Strahlen resp. durch die Emanation die Atmungsintensität der chlorophyllhaltigen und chlorophyllosen Zelle ungemein erhöht wird, namentlich, wenn in der Atmosphäre 26,2 bis 83 $ME = 10{,}506 \times 10^{-12}g. = 0{,}00001$ mg. Ra bis $33442 \times 10^{-12}g. = 0{,}0000334$ mg. Ra enthalten sind.

Die Produktion an Kohlendioxyd beträgt um 40–90 Prozent mehr, als wenn der Atmungsprozess ohne Radiumemanation vor sich geht.

Bei Verwendung von Beta-Strahlen ist es möglich, wie wir durch Experimente nachgewiesen haben, die Pflanzenproduktion zu erhöhen und zwar wird bei Gegenwart aller Vegetationsfaktoren der Aufbau neuer lebender Pflanzenmasse bis um 120 Prozent gesteigert.

Bereits vor 13 Jahren haben wir in Joachimsthal mit den Beta-Strahlen von 1,5 mg. Radium in Form von Radiumchlorid operiert und es ist uns gelungen, aus Kohlendioxyd, Wasser, und Kaliumhydroxyd künstlich Zucker nach derselben Methodik, nach welcher ich die Hexosen unter Einwirkung des ultravioletten Lichtes erhalten habe, darzustellen.

Je tiefer und tiefer wir in die Erkenntnis der gesamten Kraft- und Stoffwechselprozesse der chlorophyllosen und chlorophyllhaltigen Zelle eindringen, desto mehr sehen wir, dass die Radioaktivität eine fundamentale Erscheinung ist, deren Erkenntnis uns einmal zur Enthüllung des Geheimnisses des Lebens führen wird.

THE INFLUENCE OF H-ION CONCENTRATION ON THE TURGOR AND MOVEMENT OF PLANT CELLS WITH SPECIAL REFERENCE TO STOMATAL BEHAVIOR[1]

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The mechanism of stomatal movement once conceived to be comparatively simple has appeared increasingly complex and obscure as investigation has been extended. Weber's ('26b) recent characterization of it as "protoplasmic regulation" is only another way of stating this complexity. Nevertheless, my recent studies have led me to a rather simple theory of the primary cause, though one which is quite different from the original views. The results obtained point to the conclusion that the normal turgor changes in guard cells are, in large part, merely a specialized example of a phenomenon which is very general not only in living cells but in biocolloids apart from life, namely, changes of hydration in relation to H-ion concentration. It may be granted that the mechanism of this hydration is still obscure—a purely physical problem, however—and that it is probably not the whole cause, but is aided and amplified by oscillations in the hydrolytic synthetic balance of carbohydrate, oscillations which are also strictly regulated by the same H-ion factor.

From the pioneer work of Lloyd ('08) on the growth of pollen tubes to such recent researches as those of Robbins, many papers have been published to the effect that the volume of living cells and tissues, whether in organic growth or mere absorption of water, is a function of H-ion concentration; and the majority, though not all, record a minimum—usually to the acid side of the neutral point—lying between two maxima. If complications could be eliminated we should expect the swelling curve of a living cell, plotted against pH, to be a composite of those of its various components. But without further evidence it would be unjustifiable to assume that such a bimaximal curve whether of growth or water uptake is dominantly one of imbibition by an amphoteric colloid, since pH optima characterize all sorts of reactions, enzymatic and otherwise, that may modify turgor.

One must combine with experiment a close scrutiny of cytological changes if one is to discover by what mechanism or mechanisms each particular type of cell undergoes its turgor changes. Therefore, while part of the present work consists simply of demonstration of the relation between volume and pH, a part is devoted to such a study of mechanism.

Reagents. Our object is to vary the internal pH, but, since it is not feasible— on account of adsorption of indicators, among other reasons—to measure the

actual pH in any part of the cells themselves,[2] one has to be content with using readily penetrating reagents (acetic acid and ammonia in this case) accompanied by measurement of the pH of the medium. Unbuffered solutions in relatively large volume were employed, and the pH was approximately determined by the colorimetric method.

Both in the case of guard cells and of *Spirogyra*, strong acid and alkali proved very uncertain and slow in producing any effect. With the alkalies particularly (KOH and NaOH) penetration, short of injury, appears to be almost negligible.

Our main theme—an account of stomatal behavior—is prefaced, for purposes of comparison, by a few experiments on *Spirogyra*.

A. SPIROGYRA

To allow of variation in volume of the protoplasts they are shrunk from the wall by hypertonic cane sugar, 0.4 or 0.5M, in which various concentrations of dilute acetic acid and ammonia are included. The material used, *Spirogyra submaxima*, plasmolysed smoothly, the vegetative protoplasts taking the form of a cylinder with hemispherical ends and the zygotes that of a sphere. Volume was therefore easy to calculate from linear measurements.

Ammonia above a certain concentration, about $M/4000$, begins to cause a dense plastic precipitate, which includes the tannin content of the cells. The presence of this precipitate and its condensation under the action of surface tension interferes apparently with swelling or even tends to cause shrinkage of the protoplast. Therefore, cells with a minimum amount of precipitate were selected for measurement, but in the case of the zygotes its concentration was too great to avoid the complicating effect in this way, so that the values for the volume of the zygotes in alkali are relatively more affected. Allowing for this it is probable that in alkali as in acid the non-vacuolated zygotes undergo greater proportional change in volume than the vacuolated vegetative cells.

The following table summarizes the results. Each volume recorded is an average of many readings, but the individual variations are so great that the actual figures signify little. The general trend however is obvious.

TABLE 1. VOLUME OF SPIROGYRA CELLS (PLASMOLYSED) WITH M/2 SUCROSE IN DITCH WATER) IN RELATION TO H-ION CONCENTRATION. 1–2 HOURS EXPOSURE.

	Acetic acid				H₂O	Ammonia			
Concentration	$\dfrac{M}{4000}$	$\dfrac{M}{8000}$	$\dfrac{M}{16,000}$	$\dfrac{M}{32,000}$		$\dfrac{M}{8000}$	$\dfrac{M}{4000}$	$\dfrac{M}{2000}$	$\dfrac{M}{1000}$
Approx. pH	4.1	4.5	5.5	6.2	7.0	7.8	8.5	9.0	9.3
Vol. veg. cells	112	106	102	98	100	102	108	118	130
Vol. zygotes	135	130	107	100	100	100	105	115	125

[2] See footnote page 1158.

It will be seen that there is a zone between limits at pH 5.0 to 5.5 and about pH 8.0, respectively, in which there is little variation in volume, while there is a considerable increase as the pH is extended on either side of this region. Whether there are two minima, one toward each end of this flat zone, requires more extended measurements to decide.

The variation in volume is not great in the above case but *conjugating gametes* may be induced to undergo very notable changes by a similar variation of pH. Gametes or parthenospores in active contraction may, on addition of dilute ammonia or acetic acid, expand till they refill the cell even though it should involve a 100 per cent increase in volume. It is to be noted, however, that acid and alkali inhibit the excretion of water by the contractile vacuoles described by Lloyd and thus allow endosmosis to play its normal part.

Mechanism. Enough has been said to demonstrate that the H-ion factor acts in a complex fashion. Further discussion is postponed until the case of the guard cells has been described. One important connection however which we shall find in the latter appears to be absent in *Spirogyra*. No relation could be detected between H-ion concentration and starch content.

B. Stomata of Zebrina Pendula

1. stomatal movement in leaf sections with the pH varied experimentally

The guard cells of stomata are specialized both to undergo great changes in turgor and also to endure an unusual range of H-ion concentration. They are thus peculiarly suitable objects of experiment in investigating the relation between these two factors.

Tangential sections were taken from the under side of the 2nd. or 3rd. leaf of *Zebrina pendula*. In the first set of experiments these were kept in covered vessels of acetic acid and ammonia of various concentrations usually for 6 to 20 hours, and at the end of that time or at intervals the total diameter and pore diameter of a number of stomata were measured. The pH of the solutions was determined both at the beginning and end of the immersion.

In figure 2 is shown the relation to final pH of the pore diameter (left) and stoma diameter (right). The units for the latter are graded arbitrarily to fit those for the former and are included chiefly in order that the lower curve may be extended below the limit at which the pore becomes completely closed.

(1) *Stomatal posture and turgidity.* The form or posture of the stomata is seen to vary conspicuously with H-ion concentration. The measurements indicate minimum turgidity between pH 5.0 and pH 5.5, though there is little variation between pH 5 and pH 7.5. Turgidity increases greatly in alkali up to the limit of toleration (which is surprisingly high) and to a less extent in acid. Intact stomata become or remain closed in the middle pH region, open widely in alkali and less widely in acid. Stomata with the auxiliary cells disrupted do not close completely at any pH but have a wide amplitude of movement. Nicolic ('25,) has previously investigated the action of acids, using a different method. The
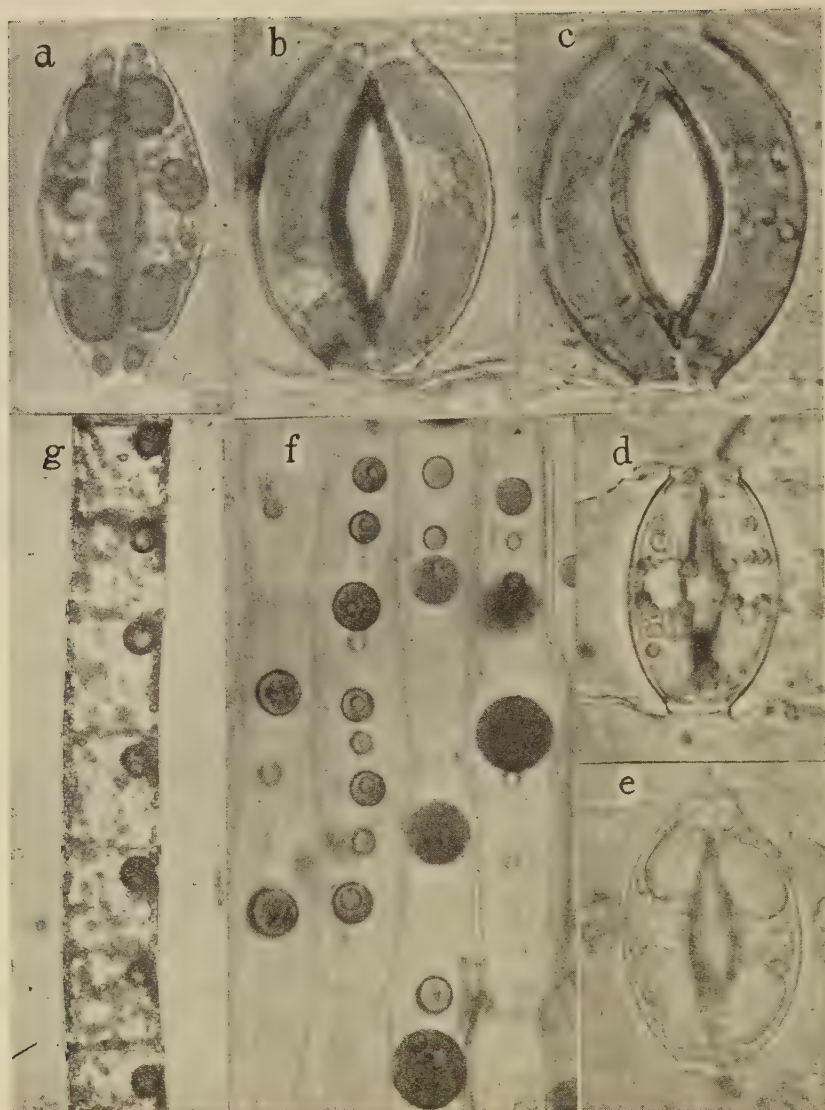
Fig. 1. (a) Stoma of *Zebrina*. The vacuome, stained deeply with neutral red in distilled water, has divided into several droplets. Stoma closed.

(b) The same in dilute NH_4OH The portions of vacuome have expanded and fused to a large extent Stoma partially open.

(c) The same in a slightly higher concentration of NH_4OH. The vacuome is further enlarged and fused into a single vacuole covering the nucleus. Stoma wide open.

(d) Unstained stoma in M/4 cane sugar. The vacuome in each guard cell consists of 2 portions

(e) The same in M/4 cane sugar, plus acetic acid, pH about 4.5. The portions of vacuome have a greater tendency to reduce surface. In all of the above the position of the chloroplasts is seen to be largely determined by the pressure of the vacuome.

(f) Epidermis of bulb scales of onion. deeply stained with neutral red and treated with weak NH_4OH. The droplets of precipitated vacuolar colloid show vacuolization under the action of the alkali.

(g) *Spirogyra* stained with neutral red and treated with caffeine. The precipitate of sap colloid has fused into a single drop, which, like the droplets in (f), expands in alkali and expands and disperses in acid.

effects of alkali here described do not appear in the literature (Iljin '22, who used only strong alkali and acid, and these in combination with salts, etc.). Similar series of measurements were made when the external medium containing the acid or alkali was 0.125 M to 0.25 M cane sugar (Fig. 4), but these add nothing essentially new to the relations summarized in figure 2, in which distilled water is the medium. The osmotic equivalent of the sap concentration at incipient plasmolysis was found to range from about 0.2 M sucrose at the pH of minimum turgor to at least 0.75 M in M/1000 ammonia, say pH 9.5.
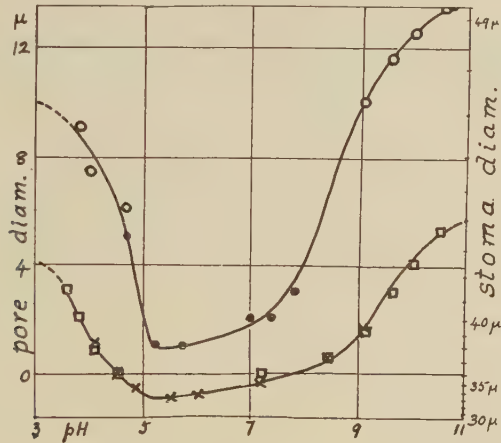
Fig 2   Stomatal posture in relation to pH, using acetic acid and ammonia   Upper curve, stomata with auxiliary cells disrupted. Lower curve, stomatal apparatus intact.   ○□ pore diameter after 6 hours exposure; □ pore diameter after 20 hours exposure; × stoma diameter after 20 hours exposure.

(2) *Starch content*. (The number and especially the size of the starch grains was compared after treatment with iodine in KI). There is also a correlation, when equilibrium is attained, between the pH of the medium and the amount of starch in the guard cells. Starch is abundant in the pH region of closure (maximum amount about pH 5.0) and dwindles to imperceptibility in regions of greater opening. Its disappearance is much more rapid in alkali than in acid.

(3) Whatever the condition of the stoma as regards posture and starch content at the beginning of the experiment, the final result at any pH is approximately the same. With regard to starch in the guard cells, therefore, it appears that equilibrium of hydrolysis and synthesis depends mainly on the H or OH ion concentration instead of simply on the concentration of the respective products, as in a typical catalytic process. The acid and alkali must themselves enter into the reaction to shift the equilibrium so profoundly. A simple enzymatic mechanism seems to be insufficient explanation. This applies to any other hypothetical enzyme action as well as that of diastase.

(4) *Flaws in the correlation between posture and starch content*. In spite of the fact that both the posture and starch content of the stomata are closely correlated with pH, the correlation between the two former features themselves is not

so complete that opening and closing can be entirely due to hydrolysis and synthesis respectively. Here our conclusions diverge from current views as to the rôle of oscillation in starch content. The lack of correlation is shown thus for example:—

(a) Rapid changes of posture (notable within less than half a minute) follow changes in pH, while it takes one to several hours for a perceptible change in the amount of starch (Fig. 3, *a* and *b*).

(b) Turgidity and posture vary with pH even though starch is completely hydrolysed. Example:—

NH_4 OH (20 hrs.)	M/2000	M/1000	M/500
pH at start (approx.)	9.0	9.5	?
pH at close (approx.)	8.0	8.5	9.0
pore diameter, μ	8	10	12
starch content	0	0	0
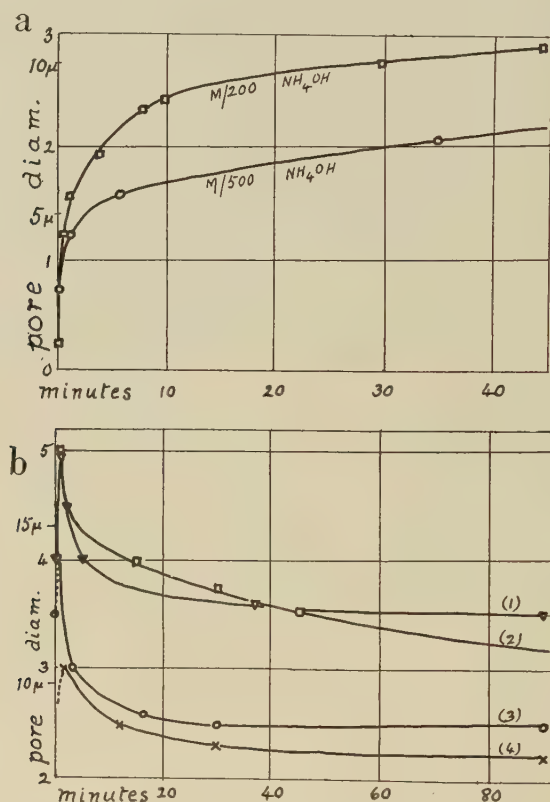
Fig. 3. Rate of stomatal movement in response to pH change.

(a) (above) Tangential leaf sections with the stomata closed and containing abundant starch put into solution of NH_4OH. Rapid opening of stoma. Starch disappears only after several hours.

(b) (below) Open stomata 1, 2, 3 and 4 without starch put into aq. dist. pH 5.5. After momentary expansion partial closure takes place rapidly. Starch formation is slow—no starch is visible in stoma (3) after 90 minutes.

(5) Evidence is accumulated that the mechanism through which variation in H-ion concentration primarily acts is its direct effect on the vacuome (= vacuolar system, Dangeards' useful term). This contains an amphoteric colloid the hydrophilic property of which appears to vary with the reaction. Briefly, the evidence for the existence and special rôle of this colloid in the vacuome is as follows:—

(a) The vacuome in *Zebrina* has an opalescent appearance as if rich in suspensoid matter.

(b) It strongly absorbs basic dyes on the alkaline side of pH 5.0 to 5.5 and changes from basophil to acidophil on the acid side of this region, indicating amphoterism. This is true of other plants also so far as they have been tested.

(c) Deep staining with basic dyes causes the vacuome to break up into drops or irregular masses and these expand under the influence of either acid or alkali. In the latter particularly they may be seen to coalesce and to fill the greater part of the cell, evidently exerting pressure (Fig. 1).

(d) In the auxiliary and other epidermal cells and in many other types of cell, including *Spirogyra*, similar combinations of colloid (especially when tannin is present) with basic dye condense as droplets *within* the vacuole, (as perhaps it does sometimes in guard cells also. These drops themselves expand greatly, frequently with vacuolization, in presence of ammonia; and they expand or disperse throughout the vacuole in presence of acid. Thus we see that acid and alkali may act directly on sap colloid to produce volume change. We do not pretend to understand the physical mechanism by which these

droplets take up and lose water, but merely argue that, whatever it is, it should apply equally to the vacuole as a whole. The analogy as regards the pH relation to the swelling and osmotic pressure of protein is suggestive, but the fact that when ammonia is applied the absorbed fluid may be segregated as poorly stained "vacuoles" within the deeply stained substance of the parent globule—which vacuoles burst and reform in typical contractile fashion—and that there is probably an enveloping film with membrane qualities (Scarth '26), lead one to speculate on the possibility of an electro-osmotic mechanism. It is of interest to note also that chloroplasts in general possess the same property of immense swelling with vacuolization in presence of ammonia.

(e) Apart from staining, the vacuome changes its form and volume with a shift of pH (Figs. 1 and 4). (The unstained vacuome is best observed when it has been somewhat shrunken by raising the osmotic pressure of the external medium).

While the volume of the vacuome increases both in acid and alkali, its form is different in the two cases. In alkali the surface tension at the vacuolar interface may be judged to be reduced and in acid to be increased. At least the tendency in the former is for the vacuome to follow the contour of the cell and to form two rounded masses in the latter (Fig. 1). The variations in pressure and form of the vacuome produce alteration in the form of the nucleus and position of

the chloroplasts corresponding in large measure to those described by Weber ('25) for normal stomatal movement.
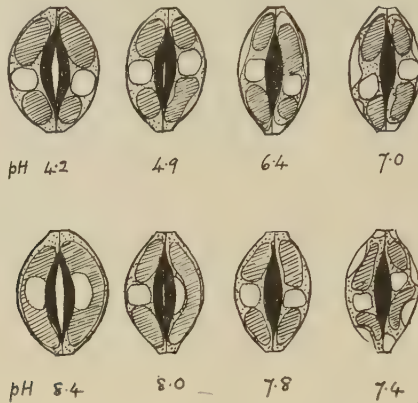
Fig. 4 Diagram of stomata (chloroplasts omitted) in M/4 cane sugar at varied pH. Note (a) plasmolysis pH 6.4 to 7.4 with greater adhesion to wall in alkali; (b) relative turgidity of guard cells and tendency to open in relation to pH; (c) expansion and fusion of vacuome in alkali; expansion with rounding off in acid.

II. Stomatal Movement on the Plant Under Normal Conditions

(1) In the ordinary daily cycle of movements of the stomata of *Pelargonium zonatum* a change of reaction is clearly shown by a color change in absorbed neutral red dye. When first the dye is absorbed naturally open stomata are relatively alkaline (yellow orange) and closed stomata (taken from the dark) relatively acid (pinkish red). Later both become orange red in a solution of the dye in plain water. The only definite statement the writer has seen as to a change of reaction during normal movement is that of Sayre who states that acidity changes—but does not say in which direction—in *Rumex Patientia*. More indefinite changes of tint were observed in some other plants, but in *Zebrina* and most of the types examined the indicator is too strongly adsorbed to function properly.[3] A concentration of ammonia so high as to be toxic is necessary to produce marked yellowing of neutral red in *Zebrina*; a rather high concentration is also required to change the color of the natural pigment which the guard cells of this plant contain. We may assume that such a degree of alkalinity is not attained under normal conditions.

(2) There is indirect evidence, also, of a similar change of reaction in all varieties of guard cell inasmuch as the same morphological and physiological distinctions exist between normally open and closed stomata as between those which have their posture determined by alkaline or slightly acid media respectively. This distinction is seen with regard to the following:

(a) Starch content (Darwin '97, Lloyd '08, Iljin '22).

[3] Later experiments with non-adsorbed indicators show that the vacuole of the guard cells may range from about pH 4.5 on plants kept in the dark to about pH 7.0 on plants exposed to full sunlight.

(b) Adhesion to the wall on plasmolysis. This is greatest in alkali as it is in normally open stomata (Weber '25*a*).

(c) Heat resistance—least in acid (Lepeschkin '24) and in the case of normally closed stomata (Weber '26).

(d) Internal morphological changes. These have been briefly referred to above and are similar under normal and experimental conditions.

The conclusion is that normal movements are governed by the same changes of H-ion concentration within the guard cells as proved effective under our experimental conditions.

(3) The origin of these H-ion changes is suggested by the relation to light (Kohl '86) and to variation in CO_2 content (Darwin '97, Lloyd '08, Linsbauer '16). The fact that light causes opening and especially that only those wave lengths of light are effective which are active in photosynthesis, coupled with the fact that all functional stomata contain chlorophyll, points irresistibly to photosynthesis as the antecedent of opening. But the active agent cannot be a product of photosynthesis as was once supposed, since light acts equally well or better in absence of CO_2. Since also absence of CO_2 by itself is sufficient to produce opening we conclude that photosynthesis acts through removal of CO_2. The results above obtained as to the effect of change of reaction on stomatal posture indicate that the reduction of CO_2 during photosynthesis is really effective in producing opening because it allows the development of an alkaline reaction within the vacuome, and that the increase of CO_2 during intermission of photosynthesis and continuance of respiration causes closure because it increases acidity.

The rule that stomata open in the light and in proportion to its intensity, and that they close in the dark meets with certain common exceptions which require explanation. Further investigation of these is necessary but it is not improbable that they may turn out to be "the exceptions which prove the rule".

There is first the common discrepancy of early closure, that is, during the day. Much of this may be ascribed to incipient wilting (see later) as Loftfield ('21) argues, but as it is doubtful if this cause can always be invoked, and as the closure appears to be favored by high insolation, the suggestion is here made that it may sometimes be due to inhibition of photosynthetic activity through accumulation of its products.

Secondly, there is the discrepancy of opening during the night or in prolonged darkness. Correlated with this is the occurrence of a starch minimum during the night (Alexandrow '25) partly confirmed by Strugger and Weber ('26). It is now suggested that this opening and starch reduction are the result of a temporary excess of CO_2 and high acidity.

(4) As to the mechanism through which the change of H-ion concentration acts under normal conditions it appears probable from the speed with which opening takes place in some plants on access of light as compared with that of starch reduction, that the more rapid hydration changes in the vacuome are again an important factor. It may be argued that other more speedy enzymatic reactions than the digestion of starch may be involved, but, if so, we are still left

with the problem of their peculiar relation to H-ion concentration as emphasized above.

(5) The rate of stomatal movement varies with the plant, however. It is particularly rapid in *Zebrina*—the guard cells of which contain much colloidal material; it is much slower in *Pelargonium* where the colloidal content, or at least dye absorption, is correspondingly less. Probably, therefore, plants differ in the relative part played respectively by colloidal imbibition—or whatever the hydration mechanism is—and by the osmotic pressure of hydrolysed carbohydrate in developing turgor of the guard cells.

(6) Additional factors undoubtedly enter into stomatal movement on the plant, but the indications are that their part is subsidiary. Brief reference to these must suffice.

(i) *Variations* (probably) *in the turgor pressure of the auxiliary or neighboring epidermal cells.* [Leitgeb ('88), Ursprung and Blum ('24), Weber ('26)]. Considering the amplitude of movement under the conditions of experiment of stomata in which the auxiliary cells were either eliminated or acted in opposition to the guard cells, this factor does not appear to be one of prime importance to say the least. Pressure by the adjoining cells is certainly necessary for complete closure but need not vary.

(ii) *Addition to or substraction from the carbohydrate in the guard cells.* The carbohydrate cycle in these cells cannot be a closed one. If photosynthesis adds, exo-diffusion must take away. Lloyd has also cited evidence of endo-diffusion. Diffusion requires permeability, and, in as far as the cells are permeable to the soluble carbohydrates, these solutes will fail to exercise an effective osmotic pressure. If, therefore, the oscillations in starch content are to have the significance that they appear to have in helping to regulate turgor we must further postulate—

(iii) *Changes in permeability for sugars.* It cannot be said that these have been proved to occur, however. Kisselew's results purport to demonstrate such changes but are all open to other interpretations (Weber '26*b*). Further experimentation is necessary on this question and generally on that of the effectiveness of the soluble carbohydrates in promoting turgidity of the guard cells.

(iv) *Variation in turgidity of the leaf as a whole.* Only extreme variation has any effect, and whether this has any important direct action is uncertain although the relatively greater liability of guard cells to injury through wilting may indicate a relatively greater liability to water loss. It is probable however if Steinberger's ('22) observation is correct, namely, that the osmotic value of the guard cells *falls* on wilting—that the action is indirect. In harmony with the normal mechanism it may be suggested that deficiency of water inhibits photosynthesis (Dastur '24) with the normal consequences on stomatal movement and starch synthesis. It would appear, therefore, in the light of our present knowledge that the part played by factors apart from H-ion change is either slight or problematical.

In conclusion I may recapitulate what appears to be the series of events that brings about opening and closure in the natural state.

i. The morning light initiates photosynthesis resulting in a reduction of CO_2 concentration and the development of a more alkaline reaction within the guard cells. In response to the change of reaction the vacuome apparently in virtue of its colloidal content quickly imbibes more water from the adjacent cells and causes distention of the guard cells. More gradually, as a result of the same H-ion change starch is hydrolysed, and unless the cells are freely permeable to the soluble product—a point still *sub judice*—turgidity will be further increased thereby.

ii. Cessation of photosynthesis whether from lack of light, accumulation of photosynthetic products (?), or wilting (?) is followed by a similar series of opposite changes.

iii. Prolonged closure in darkness may possibly result in sufficient acidity, through accumulation of CO_2, to cause temporary opening along with slight hydrolysis of starch.

This theory has an element of interest to the general biologist in the bond of similarity that it provides between the ventilatory system of plants and animals, for utterly different though the physical mechanism of gas exchange is in the two cases, the regulating chemical factor is declared to be the same. Plants however, in virtue of their special rôle in nature, are so adapted as to regulate for a deficiency as well as for an excess of CO_2.

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Only critical references are here included. See Weber 1923 and 1926[b] for a fuller literature.

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THE PROBLEM OF EXCRETION WITH ESPECIAL REFERENCE TO THE CONTRACTILE VACUOLE[1]

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Contractile vacuoles (as also pulsating vacuoles) have hitherto been regarded as occurring only in the protista and in the motile forms of plants (fungi, algae), in which they have been variously considered as more or less specialized organs or organoids. It has recently (Lloyd '24, '26) been made clear, however, that contractile vacuoles occur in the conjugating gametes and in the condensing zygote of *Spirogyra* (and this is probably true also of other *Conjugatae*). Furthermore, they may be induced in vegetative cells by the application of suitable strong plasmolysing agents (Lloyd and Scarth '26). Thus it is indicated that these organoids may occur much more widely than hitherto supposed.

The distinction between contractile and pulsating vacuoles rests on whether rhythmic behavior from a constant primordium occurs or not. The observed repeated appearance of contractile vacuoles from the same point in the cytoplasm,[2] and inferentially from the same primordium in *S. longata* and in *S. Weberi*, permits us to describe some of the contractile vacuoles of *Spirogyra* gametes as pulsating vacuoles, this having been observed more recently by me also in *S. submaxima*. That, however, a primordium really persists may be questioned, even though, as in numerous forms, the pulsating vacuole repeatedly appears at the same point. Similar appearances to those described by Metcalf ('10) and by Mast ('25) in *Amoeba* are afforded by *Spirogyra*, in so far as, in *Spirogyra* sp. with richly granular cytoplasm, there is a collection of granules ("cytomicrosomes," whatever they are) about the contractile vacuole. These granules are fewer or may not be visible in species with very homogeneous and tenuous cytoplasm (for example, *S. Weberi*), though on fixation by iodine or other suitable reagent, they become visible by the dehydration or coagulation of the contiguous cytoplasm. It would appear that a simple explanation for the accumulation of granules in this position is solely the result of their being pushed aside by the expanding bubble, the granules finding a minimal energy relation in this position. On contraction they follow the vacuolar surface, while upon reformation and expansion additional granules are picked up. This is, indeed, scarcely more than a restatement of Budington's conclusions quoted by Metcalf (p. 307 of his paper).

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[1] Presented before the International Congress of Plant Sciences, under the auspices of the Section of Physiology, Ithaca, New York, Aug. 18, 1926. Owing to the diverse interests of the audience, the presentation consisted of a series of photographs and two motion pictures illustrating (1) conjugation in *Spirogyra*, and (2) the feeding habits of *Vampyrella*, with detailed explanations. The specific paper prepared under the above caption was read by title and submitted for publication.

[2] In the motion picture of *S. Weberi* in conjugation exhibited, this was shown to occur.

That a new vacuole originates from the primordium of an exploded one is a different point on which the matter of granules has only indicatory value, as Metcalf inclines to say. In more specialized non-cellular organisms, as Nassanov ('24) and Young ('24) have recently emphasized, the contractile pulsating vacuole may take on an extremely complicated form and appear as a permanent organ, as in *Paramecium*. Nassanov finds the membrane of such organs strongly osmiophil, but Scarth and I have failed to find this to be the case. In living material (Science **63**: 459. 1926) the vacuoles were observed to arise within "myelin bodies" (Scarth: in press) which are observable as cytoplasmic extensions displaying negative surface tension due to the *external* distribution of lipoid. The manner of discharge of the contractile vacuole demands the display of positive surface tension at the membrane/fluid-within-the-vacuole interface. I must refrain from considering in detail the chrondriosome question, save only to indicate that the bodies observed by Scarth and myself simulate the forms assumed by the Golgi apparatus, whose identity with the contractile vacuolar structures in certain non-cellular forms has been argued by Nassanov ('24) (see also Bowen '26). The specific committal that vacoules originate in locations at which a colloidal substance (metachromatin or analogous material) has been secreted by the cytoplasm, a view which in a purely speculative way I have myself entertained, is that of Guilliermond ('24) and of Dangeard ('23). The material in question, by absorbing water and swelling, furnishes a starting mechanism. In the case of *Spirogyra* I have no evidence on this point to offer, but one may remark that the appearance of contractile vacuoles only at the incidence of sexual reproduction supports the view of Pfeffer of their *de novo* origin, especially as they may be experimentally produced at any time, although one is aware of Dangeard's opposite view, which might be held consistent with the behavior of *Spirogyra*.

On the other hand, regarded from the biophysical point of view, the problem of the origin of the contractile vacuole would seem to be the problem of internal syneresis. We have indeed a model which, so far as we can at the moment see, acts precisely in the fashion of the contractile vacuole. Such a model may be artificially procured within the central sap cavity of, for example, the epidermal cells of *Allium* bulb-scales. The colloidal material of the sap when treated with basic dyes condenses into drops with or without the addition of ammonia or an alkaloid (such as caffein). I observed that the addition of ammonia (if not previously present) induces the formation within these droplets of vacuoles which enlarge and burst rhymthmically, to all appearances as do contractile vacuoles in cytoplasm. Many years ago I observed the same to occur in droplets of tannin-caffein ppt. within the sap cavities of such cells as bear tannin (*Rosa* epidermis, *Quercus* cotyledons, etc. this among numerous bizarre behaviors procured by various reagents (Lloyd '12). Such behaviors seem to indicate that there is no necessity to assume that some sort of organized nuclei (here meaning centers of formation) must be previously present. The gas vacuoles of the Cyanophyceae would seem to have the same sort of origin. Equally with water vacuoles, the idea of organized centres is superfluous, but rather we may regard gas vacuoles to originate as in the following model. If a piece of crude rubber is allowed to swell

in carbon tetrachloride to which piperidine has been added[3] and then is allowed
to lose the solvent by volatilization, the interior of the mass will, as I have ob-
served, soon be found to be filled with gas vacuoles. It may well be considered
that the understanding of this model may furnish an explanation of the bio-
logical condition.

The contractile vacuoles of *Spirogyra* gametes arise in or from the cytoplasmic
layer, and reach various sizes up to approximate spheres two-thirds the diameter
of the cell. The outward bursting depends on the relative surface tension rela-
tions, as already set forth (Lloyd, '22, '26). Their function is to take water out of
the central vacuole and expel it more rapidly than it can be taken up osmotically.
To what extent other substances escape or are thrown off simultaneously has not
finally been made clear. It is certain, however, that the tannin content of the sap
is retained; for (1) the alkaloid test (caffeine) shows that vacuolar activity pro-
ceeds unabated in the presence of caffeine, which easily penetrates, but there is
never seen any precipitate in the contractile vacuoles, though the length of time
they are exposed to the reagent is sufficient to permit precipitation unless it were
shown that the contractile vacuolar membrane is impermeable to the reagent,
and this can hardly be true; and (2) the tannin-caffeine precipitate is not reduced
during conjugation, being equally abundant in the zygote as in the gametes in
whatever stage of conjugation. The presence of caffeine does not inhibit gametic
union; indeed, it may be found that, by precipitating the tannin, and thus lower-
ing the concentration of solution in the central vacuole, it hastens condensation
of the gametes again, the cobalt-sodium-hexanitrite reagent (Lloyd '25) similarly
discovers little if any reduction in potassium content, though my evidence on
this is not unequivocal. As a last consequence of contractile vacuolar activity the
central vacuole disappears. What then becomes of the solutes? They may be
taken up by the cytoplasm, and in the case of the tannin-caffeine precipitate
(caffeine-tannate) this can be observed to be the case. The behavior is the re-
reverse of what must occur when vacuoles appear in non-vacuolate embryonic
cells when the solutes are derived from the cytoplasm. They may, however, be
expelled wholly or in part. Plasmolytic tests have yielded certain indications,
namely, that the contractile vacuoles contain sap of higher concentration of
solution than that of the central vacuole. We must observe too that contractile
vacuoles are induced by treatment with plasmolytes of high concentration if they
penetrate; if, on the other hand, they do not penetrate, they cause the vacuoles
to disappear. I found also that a 6 per cent dextrose plasmolyses the fused but not
yet condensed gametes, and inhibited but did not eliminate the contractile vac-
uoles (Lloyd '26, Pl. 1, Fig. 7), but it is a matter of doubt that they might not
have resumed activity, as it was observed at another time that a $M/3$ cane sugar
solution slowed up the formation of contractile vacuoles; there were also fewer
of them formed but they were not all prevented from appearing and bursting.
Still less effect was observed by lower concentrations ($M/10$ and $M/5$), the effect
of these being inappreciable. It would seem, therefore, that the sap of the contrac-
tile vacuoles is of higher concentration than that of the central vacuole, the latter

[3] An experiment done by my colleague, Professor Whitby.

having been observed to have been lowered during maturation (Klebs '93, Czurda '24, Lloyd 24). We must not forget, however, that there is a lowering of the osmotic pressure of the gametes before the contractile vacuoles appear (Klebs, Lloyd, Czurda) and this even when permeability of the gametes is decreased (Lloyd). We have supposed this to be due to the change of sugar into starch, but it is not now certain that this is really what happens.

The function of the contractile vacuoles in *Spirogyra* is, I believe, clearly and dominantly water excretory, and may be compared more especially to the numerous water-excretory vacuoles in *Vampyrella* which are at maximum activity in animals plethoric with water after feeding on *Spirogyra* (Lloyd '26). It is well known that, analogously, the contractile vacuoles of various forms (*Amoeba*, *Euglena*, etc.) as shown by Klebs ('93), by Massart ('91), and by Zuelzer (through Calkins '26) vary in regard to their size and activity inversely to the concentration of the medium; that is, their activity is greatest when the water-plethora might supervene the more quickly. But although the chief excrete is water, in no case is water alone excreted, and, as shown above, the contractile vacuoles of *Spirogyra* appear to contain fluid of appreciable concentration. Even the water exuded by the hydathodes of grasses is not pure, as J. K. Wilson (1923) has shown, containing as it does 220 to 1030 part per million of solids. There is, however, no doubt that the contractile vacuoles of many Protozoa excrete solid material with the water. I have observed *Amoeba* thus discharging rather large, irregular masses, not, however, identifiable with those of which Metcalf ('26) speaks. Granules may sometimes be extruded by a bursting contractile vacuole in *Amoeba*. Very obvious, also, is the extrusion of very numerous granules simultaneously by the whole surface of the body by *Vampyrella* during feeding; and this can hardly be regarded otherwise (Lloyd l. c.)[4] than a case of excretion of solids probably accompanied by much in solution.

I would conclude then that the contractile vacuole is an excretory organ. It may be merely water-excretory, serving to regulate the osmotic pressure of the cell as some authors have argued (see Calkins '26, p. 170); or solids and solutes may be therewith expelled, and in this I agree with Nassanov, who states:

> In this connection I may mention the following observation in *Actinosphaerium*. Immediately following the bursting of a contractile vacuole, as its wall disappears, there is an eruption from its proximal inside surface. This appears as an outshooting of numerous cytoplasmic (?) processes, looking as if a handful of pebbles had been thrown into a pool of water. I have seen no description of this The erupted matter looks like the "protoplasmic papillae" recently described by Siefriz ('26) but they are of very brief duration, less, certainly not longer, than a second of time. The obvious idea that this is an excretion mechanism requires investigation.

As a mechanism, aside from the capacity of the contents to excrete water, the contractile vacuoles of *Spirogyra* and *Amoeba*, *Vampyrella*, *Arcella*, and the like, are identical, I believe. And though we do not speak of such in the more specialized cellular animals and plants, there are tangible grounds for believing that this mechanism may occur in all groups; that it does, in fact, serve for the

[4] I am informed by Professors Maximov and Issatschenko that *Vampyrella* has been much studied by Gobi, whose studies have been up to the moment inaccessible to me.

extrusion of water and contained solids or semi-solids in many glandular cells (though this does not imply that other methods do not occur). A notable example has been afforded by Gurwitsch ('02) in his study of the epithelium of the frog kidney. In spite of the criticism of Cushny (17) there does not seem to be good reason to doubt his observations. His figures assuredly are convincing. Gurwitsch regards the vacuoles which burst into the lumen of the gland as contractile. The absence of solids cast off into the lumen under normal conditions is not argument against this conclusion, but it would be in the interest of renal physiology if a study of the living material could be made to determine the correctness of Gurwitsch's view. The technique of studying animal gland cells in living condition is very difficult, but this is much needed. Working in this field, Uhlenhuth ('25) has recently brought forth evidence which supports the idea of contractile vacuoles as mechanisms in glandular cells. He worked with living material, without using the term "contractile vacuole," but describing behavior. The literature of animal histology contains many examples of vacuolate glandular cells susceptible of this interpretation, but I have cited elsewhere the recent work of Ludford ('25) as a case in point.

On the side of vegetable cytology, one may mention glandular cells which are active in throwing off secretions, and which offer evidence of contractile vacuolar activity. As possible examples I have mentioned (in a paper in press) the cells of the egg apparatus in Phanerogamia, glandular cells of nectaries, of the *scutellum* and other secreting organs, resinogenous cells etc., all of which may eventually be shown to present this behavior.

The purpose of this brief paper is to draw attention to a hitherto unrecognized example of water excretion by contractile vacuoles, namely, in *Spirogyra* gametes and zygotes. This case is not subject to question. It is however not possible to suppose that the water discharged is not accompanied by other substances in solution or in more or less solid condition. Indeed in many forms, solids or semisolids are dominant.

It is suggested that the contractile vacuole may be found to be a widely distributed mechanism. Already there is tangible evidence in support of this idea. It is hoped that interest in this subject will hereby be stimulated.

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THE PHYSIOLOGICAL NATURE OF DROUGHT-RESISTANCE OF PLANTS[1]

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The problem of the physiological peculiarities of plants growing in dry habitats long ago provoked the interest not only of agriculturists who in the solution of this question expect to find the right way for the selection of drought-resistant varieties, but also of botanists, especially those who study questions of experimental ecology of plants. Water is one of the most important ecological factors and the types of xerophytes, mesophytes, and hydrophytes have been acknowledged to be the fundamental ecological types.

What are the peculiarities, which allow the xerophytic plants to inhabit dry and hot regions where mesophytic plants of the moderate humid climate perish from deficiency of water? Up to the present time it was accepted that the principal peculiarity of the xerophytes is their ability to expend water scantily, that is, their low rate of transpiration. This opinion is also expressed in the latest edition of the excellent text book of plant physiology of Prof. Jost ('24), where on page 82 we read that the xerophytes are "Pflanzen trockener Standorte, die Einschränkungen in der Transpiration aufweisen." A very good illustration showing how deeply rooted is the opinion that a close connection exists between xerophytism and intensity of transpiration is the work of Bakke ('14), who finds that the index of the foliar transpiring power can serve as a direct measure for xerophytism. According to this assertion, plants with an index below 0.30 must be classed as xerophytes; above 0.70, as hydrophytes; and plants having an index between 0.50–0.70 as mesophytes. With the theory of the transpiration criterion of drought resistance is combined also the tendency to find the cause of xerophytism in external morphological and anatomical peculiarities which must limit the loss of water, especially in the decrease of leaf surface, in the substitution of petioles for leaves (as in the Australian acacia), or by flat or ribbed stems (as in the cacti), in the protection of the transpiring surface by a thick cuticle, by hairs, by a waxy deposit, etc.

It was considered also that the presence of water-storing tissues is one of the most important peculiarities of xerophytes, and very often we meet with the opinion that the most perfect achievement of nature in the creation of drought-resistant plants is the case of the cacti, plants capable of remaining several weeks and even months without water.

Such a point of view, principally morphological, could, however, not satisfy men of agronomical science in their attempt to understand the nature of the drought-

resistance of definite varieties of crop plants. It is well known that the drought-resistant varieties cannot be distinguished either by their greater hairness, by their smaller leaves, or by their succulence. That is why in relation to crop plants the transpiration criterion has assumed another form, namely, that the drought-resistant plants must use less water in forming their dry substance. The relation between the dry substance accumulated and the water expended by the plant was specially termed the transpiration coefficient; American authors termed it the water requirement of plants. According to this supposition the more the plant is drought-resistant, the less must be its water requirement.

My investigations on the water relations of plants, begun in the physiological laboratory which I founded about 12 years ago at the Tiflis Botanical Garden, very soon led me to the conviction that the intensity of transpiration alone cannot serve as an index of the degree of xerophytism. For instance, in comparing the transpiration of shade plants grown on moist irrigated plots of the Tiflis Botanical Garden with the transpiration of plants from open dry rocky slopes we observed that the latter transpired 2-3 times more than the former, notwithstanding the fact that mesophytes, used in the experiments, had thin, tender leaves, while many of the xerophytes were densely covered with white hairs or with a wax deposit and had leaves considerably thicker.

Further investigations made by me and by my collaborators, have shown that high transpiration of the xerophytes is not accidental. For instance, in investigating the influence of environmental conditions on the transpiration capacity of plants we have found that most of those factors which participate in the formation of the conception of a dry habitat, namely insolation, deficiency of water in the soil, and an impeded water supply provoke such changes in the structure of the leaves as would lead to an increase of transpiration. Thus the experiments of Miss L. D. Frey ('24) have shown that plants grown in the sun have a higher transpiration than those grown in the shade. The same experiments have shown that plants grown in a dry soil transpire more intensely than those grown in a moist one. The results of these experiments were confirmed by the recent investigations of Mrs. S. I. Kokine ('26) conducted in my laboratory in Leningrad. The experiments of W. A. Alexandrov ('22) have shown that the upper leaves of the plants that develop in conditions of an impeded water supply possess a higher intensity of transpiration than the lower ones. The only exception among all these factors is the dryness of the atmosphere. The recent investigations of Miss E. V. Lebedincev ('26) have shown that plants grown in a more or less humid atmosphere possess a higher intensity of transpiration than those grown in a dry atmosphere.

Thus most of the factors forming the dry habitat increase the transpiration capacity of plants, and it therefore follows that xerophytes, with the exception of succulents which form a special physiological type, must possess not a decreased, but an increased intensity of transpiration. This is directly confirmed by the fact which was observed in the investigations of Mrs. T. A. Krasnosselsky-Maximov ('17) namely, that in the noonday hours of bright hot days such typical xerophytes as *Zygophyllum*, *Peganum*, species of *Artemisia* and others display an

enormous deficit of water attaining 30 per cent and more of the whole water re-
serve in the plant, and thus they expend more than they obtain. During the
the night, however, this deficit is replenished. These variations are well shown
in one of the graphs of Mrs. Krasnosselsky-Maximov[2]; the continuous curve in that
figure shows the fluctuation of the water content of the leaves, the broken curve
the variation of the moisture deficit in the atmosphere. From the illustration
you may observe that one of the curves represents the mirror image of the other.

These considerable fluctuations in the water content are in direct contradic-
tion to the traditional view that xerophytes expend very slowly the water they
contain.

The water requirement of plants of different ecological types was also for
three years studied in detail by me, together with my assistant, W. A. Alexandrov
(at present chief of the Tiflis laboratory)('17). We arrived at the conclusion that
there does not exist a direct proportionality between drought resistance and the
water requirement of plants, and that many typical xerophytes, as, for instance,
species of *Artemisia, Centaurea, Zygophyllum, Peganum* and others expend water
very unproductively, using on 1 gm. of dry substance about 1.000 gms. of water,
while mesophytes require only about 500 gms. Simultaneously, the same results
were obtained by the American authors Briggs and Shantz in their excellent in-
vestigation ('14).

All our investigations, begun in Tiflis and in the present time continued at
Leningrad and at the Experimental Station of the Institution of Applied Botany
in "Kamennaja Step" near Voronesh, lead us to the conclusion that the water
requirement cannot serve as a criterion of drought-resistance of plants. Evidently
the cause of drought-resistance of different plants is not founded on the economy
of water expenditure and must be searched for elsewhere.

My observation in nature, as well as the following investigations made by
me and by my collaborators, have convinced me that the principal peculiarity of
drought-resistant plants is their capacity to endure without any significant injury
a state of permanent wilting. During the driest and hottest period of the Tiflis
summer mesophytes burn out completely, while xerophytes remaining green,
stop their development, and sometimes shed a considerable part of their leaves.
Those leaves that are not shed, remain during several weeks in a state of per-
manent wilting, which, however, passes with the first autumn rains. This greater
endurance of the xerophytes to loss of water is confirmed by the observations of
Mrs. T. A. Krasnosselsky-Maximov (mentioned above) on the fluctuations in
the water content of xerophytes during the day.

These observations lead me to the conviction of the necessity of paying closer
attention to the phenomen of wilting. As has been established by the work of
the American investigators Briggs and Shantz, and later by Caldwell, we must
distinguish two states of wilting—temporary and permanent. The first may be
observed when there is yet some available water in the soil, but when transpira-
tion exceeds the supply of water to the plant; permanent wilting takes place when

[2] See figure 43, page 235 in my book "The Physiological nature of the drought-resistance of
plants" (Russian), 1925. (Cf. The plant in relation to water. London, 1929.)

all the water available is exhausted, and the plants cannot recover even during the night.

Temporary wilting can be endured without harm by all plants and it is one of the most efficient means for decreasing transpiration. My experiments have shown that during wilting the rate of transpiration decreases from 5 to 7 times. Permanent wilting represents a different picture. Very soon the root hairs begin to die, the whole absorbing system of the plant begins to suffer; further, the leaves and young growing shoots suffer irreparable injury and finally permanent wilting leads to the complete death of the whole plant, which may be observed in the open during a prolonged drought.

Not only different types and species of plants, but also different varieties exhibit a different degree of endurance of permanent wilting. Last year my co-worker T. J. Tumanov ('26) carried out some experiments with several varieties of summer wheat, contrasting their drought-resistance. After a long period of permanent wilting of more than two weeks the plants were again watered and after a few days the number of plants which recovered was counted. Among the drought-resistant varieties from 77 per cent to 94 per cent of the plants recovered, while among the non-resistant only 23-50 per cent remained alive. Thus my conviction experienced a direct experimental confirmation. This summer such experiments are being conducted on a wider scale at Leningrad and at the Kamennaya Steppe Experiment Station.

What are the peculiarities that allow the plants to endure this state of permanent wilting? Certainly an influence must be exerted by such morphological peculiarities as a thick cuticle, a wax deposit and hairs. The latter, as we have noticed, are of little consequence during transpiration which takes place when the stomata are open, but must considerably decrease the cuticular transpiration, which is the only means of water elimination by wilted plants. Water stores in the plant must also have an important significance, and not only those that are visible, thus, for instance, in fleshy leaves or stems of succulents, but also those in subterranean organs, in rhizomes, tubers, bulbs, and fleshy roots. Such water stores are often to be found in xerophytes.

However, I consider the inner physiological peculiarities to be of greater importance. Of these the concentration of the cell sap has been studied most. The first to call attention to this last fact was Fitting ('11) in his well known investigation. As numerous experiments show, an increase of dryness of the environment contributes to an increase of the osmotic pressure in the cells, but as I have shown in a joint study with Miss T. Lominadze ('16), xerophytes possess a high concentration of the cell sap which is hereditary, and this gives them an indubitable advantage in comparison with mesophytes during a permanent drought. Thanks to their higher osmotic pressure, the xerophytes are capable of developing in a wilted state a higher suction force and, besides, a high concentration of the cell sap contributes to the withdrawal of water by the sap from the protoplasm and the cell wall and thus lessens considerably the loss of water. This view is supported by the interesting observations of B. A. Keller ('26) on the transpiration of *Salicornia* grown on different concentrations of NaCl.

The capacity for enduring wilting is not quite constant in each species of plant and fluctuates considerably according to the conditions of growth. The development of plants in a moist soil or humid atmosphere or in the shade decreases their endurance considerably; on the contrary strong light and deficiency of water hardens the plants. Interesting results were obtained by T. J. Tumanov ('26) in studying the influence of repeated wilting upon plants; he found that the first permanent wilting checks considerably the growth and decreases the yield of the plant, but makes it quite insensible to further wilting and even slightly increases its assimilating and transpiring capacity. It can therefore be compared with the hardening of some plants to frosts occasioned by a lowered temperature. That is why in subjecting a plant to wilting in the early stages of development one can increase its resistance to drought at later stages. The same influence may be exerted by transplanting, which is usually accompanied by a more or less profound state of wilting.

One of the important consequences of permanent wilting, especially when it is repeated many times, is the change in the anatomical structure of the plant. The cells of the newly-developing leaves become smaller, and their number per unit of the leaf surface increases; correspondingly the stomata are reduced in size and increased in number. The venation becomes denser. This has been clearly demonstrated and illustrated by me[3] through the structure of the leaves of the sunflower. In this illustration referred to there is shown on the left the control, and on the right the plant that has been subjected to periodical wilting. Such changes in the structure I term xeromorphism, for the same peculiarities of structure, long ago discovered by V. R. Zalensky ('04) are natural to plants grown in more or less dry habitats. The physiological changes that accompany these anatomical peculiarities, as our experiments have shown, are the increase of assimilation and transpiration capacities, and as a general rule it must be acknowledged that xeromorphic leaves work with more energy then mesophytic ones.

Xeromorphic structure is induced not only by periodical wiltings. All those external factors which participate in the formation of a dry habitat, namely, dryness of the atmosphere and of the soil, strong insolation, etc. all induce analogous changes in the structure of a plant. V. R. Zalensky ('04) in his classical work concerning the structure of the leaves of the upper and lower tiers has shown that the upper leaves, which develop in conditions of deficient water supply and intensive transpiration, differ by having smaller cells and a denser venation. This last I have also pictured in an illustration[4] taken from the book of Zalensky representing the venation of the upper and lower leaves of one and the same tobacco plant. The same phenomenon was observed later by Yapp, in his investigations on *Spiraea ulmaria*. This case I have also illustrated[5] through the reproduction of one of his very striking drawings.

Our investigations have shown that the same changes are produced by the separate environmental factors. This may be seen in the structure of leaves of

[3] Loc. cit. figure 59, page 362.
[4] Loc. cit figures 52 and 53, page 327.
[5] Loc. cit. figure 54, page 333.

Phaseolus[6] grown in the light of a strong electric lamp of 1000 watts at a distance of one and of two meters from the lamp. The light which is 4 times stronger has caused a more xeromorphic structure. Of interest are the drawings of Miss E. V. Lebedincev[7] which represents the structure of the leaves of *Phaseolus* plants, one grown in a drier and another in a more humid atmosphere. Mrs. S. Kokine[8] has portrayed the structure of the leaves of *Phaseolus* grown with different moisture contents of the soil. Thus all these enviromental influences increasing transpiration or hindering the water supply, in short, causing a water deficit in the plant, lead to the same structural peculiarities of the leaves. Thanks to the denser system of veins and the lesser dimensions of the cells the xeromorphic structure insures a better water supply for the plant, and that is why the plants that possess such a structure during their developement, or those that possess it as a hereditary peculiarity, can grow better in conditions of drought. Besides, most of the xerophytes possess a large root system, many times surpassing in its dimensions the aerial organs, which also contributes to a better water supply. However, I am not inclined to acknowledge these anatomical peculiarities to be the only or even principal cause of the drought-resistance of plants. I am of the opinion that the external xeromorphism is only a manifestation of the inner physiological changes in the cells, which play a foremost rôle. One of these changes is the increase of the concentration of the cell sap, mentioned above. Besides, some preliminary data suggest that some changes occur in the colloids of the plasma so that their water-holding capacity increases considerably, as my co-worker J. Tumanov has succeeded in observing by the dilatometer method. It is possible that these inner changes in the protoplasm and in the cell sap are the fundamental processes, the primary cause of the increase of drought-resistance, while the external anatomical changes, mainly reduction in the size of the cells, are only the consequences of these inner changes.

The problem of drought-resistance of plants must thus be transferred from the domain of morphological and anatomical structures into the domain of problems of a colloid-chemical character. The problem of cold-resistance of plants has undergone the same evolution. This certainly does not make the solution of such problems easier but nevertheless brings us nearer to an understanding of the enigma.

In conclusion, I must mention the xerophytes which are not xeromorphic. A xeromorphic structure I understand to be the result of a water deficit in the plant. That is why plants which possess large stores of water in the transpiring organs, that is, in the leaves and stems, especially succulents of the type of cacti and aloe, do not possess peculiarities of a xeromorphic structure. Their cells are large, their conductive system is weakly developed, their osmotic pressure is very low. This is quite a special type, the peculiarities of which must not be attributed to other xerophytes, as is often done.

[6] Loc. cit. figure 55, page 349.
[7] Loc. cit. figure 57, page 353.
[8] Loc. cit. figure 58, page 360.

The ephemerals are also exceptions. These plants, though natural in dry habitats, vegetate only during the moist, rainy period, and we might vainly search among these plants for peculiarities characteristic of the real xerophytes, which vegetate most of their life-time in conditions of intensive transpiration and deficiency of water.

ON THE ORIGIN OF THE THERMAL FLORA[1]

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The American Naturalist, W. H. Weed, was the first who pointed out the possibility that plants found in hot springs might be the oldest organisms on the earth. In his paper on "The Vegetation of Hot Springs" printed in the year 1889, he said:

"The ability possessed by the vegetation found in such waters to withstand such extreme and adverse conditions of environment shows the possible existence of this form of life during the early history of our globe, when the crust of the earth is supposed to have been covered with hot and highly mineralized waters. Such plants may thus represent the earliest links in the chain of evolution." The Weed idea is now known as the Relict-Hypothesis.

In 1923 I pointed out in a paper given at the hundredth-anniversary meeting of the Society of German Naturalists and physicians in Leipzig that the Relict-Hypothesis is not well founded and I gave several important facts which opposed it.

Recently Molisch, in his book entitled "Pflanzenbiologie in Japan, auf Grund eigener Beobachtungen,"treated the same idea as follows:

"Bei dieser Sachlage drängt sich einem eigentlich die Ansicht förmlich auf, dass die ersten Pflanzen, die unseren Erdball besiedelten, wahrscheinlich thermophile, hohen Temperaturen des Wassers angepasste Cyanophyceen und gewisse Bakterien waren, dieselben Organismen, die noch heute die Thermen bewohnen. Die gegenwärtig in den heissen Wassern vorkommenden Cyanophyceen können als die Nachkommen, als Relikt jener Blaualgen betrachtet werden, die einst weite, mit noch warmen und heissen Wassern bedeckten Erdstriche bewohnten und die nach eingetretener Abkühlung der Erdrinde in den aus der Vorzeit Zurückgebliebenen oder neuentstandenen Thermen eine willkommene Zuflucht gefunden und sich bis auf den heutigen Tag erhalten haben."

Molisch connected the relict-hypothesis with the question of the origin of the first organisms on the earth. He drew the following conclusion "dass die ersten auf der Erde aufgetretenen Lebewesen thermophile Schizophyceen gewesen sind d. h. gewisse Bakterien und insbesondere Cyanophyceen, die verhältnissmässig hohen Temperaturen angepasst waren, die Wässer der damals noch warmen oder heissen Erdrinde bewohnten und deren Nachkommen sich bis auf den heutigen Tag in den Thermen erhalten haben."

The main idea of the relict-hypothesis appears very obvious, and because of that it was very deceiving for the biologists. There are now, however, several

1176

reasons which seem to justify me in abandoning my previous undecided position towards the hypothesis and to come out against it. That position has been taken already in the case of *Mastigocladus*. It was shown that this alga is not a relict form but that it is only an organism adapted to high temperature. At present the reasons seem to be conclusive enough for a general inference that all thermal vegetation consists of a flora adapted to high temperature. The reasons referred to above are these:

In making the hypothesis, Weed assumed that the flora of different, widely distributed thermal springs is in general the same. That this is not the case has already been shown by West, and later confirmed by Elenkin. My own investigations on the thermal flora of Croatia demonstrated that neighboring hot springs have different vegetation. It has been shown that the thermal vegetation depends not only on the temperature but on other factors also, especially on the chemical composition of the water.

It was shown by Elenkin that the thermal flora of Kamtchatka is very rich in Cyanophyceae, consisting of the following:

(1) A very few cosmopolitan species, found in hot springs throughout the world; (2) a considerable number of species found in hot springs of the moderate and arctic regions; (3) forms known as yet only from cold waters; and (4) many new forms.

Wilhelm found also that the vegetation of the thermal springs of Czechoslovakia consists of a large number of forms which are common to cold waters.

Molisch has not as yet given the list of algae of Japanese thermal springs but from his biological paper it can be seen that in the thermal springs of Japan there occur many Cyanophyceae normally found in cold waters. He is of the opinion that the number of cosmopolitan forms among the thermal algae is much higher than assumed by Elenkin.

It was mentioned by Weed that Archer observed in the thermal springs of the Azores fresh water algae common to fresh waters of Great Britian. West also found a different algal flora in different hot springs of Iceland. He compared this flora with that of tropical Africa, as described by Schmiedle, and found two species to be identical (*Mastigocladus laminosus* and *Phormidium laminosum*) While the comparison with the flora of Yellowstone revealed only one (*Phormidium laminosum*). For a better understanding of this question it will be necessary to make an extensive comparison of different lists of the thermal floras. It is possible now to make the following statement: (1) The thermal floras differ in the species of algae they contain. (2) Most of these species are also commonly distributed in cold waters. (3) There are, however, certain thermophilous forms which are found in many thermal springs. But there are, to my knowledge, no specific genera or species limited to thermal springs. Also, the much discussed *Mastigocladus* has a cold water form as its closest relative. (4) So far no alga, nor any other organism, has been found with the distinct characteristics of a relict form, as would be expected according to the relict-hypothesis. (5) Most investigations on thermal biology agree that the *Cyanophyceae* are most important among the organisms found in thermal springs. Moreover, in some therms they

are almost the only plants present.   On the other hand, in some thermal springs of the Azores, Iceland, Kamtchatka, and Yellowstone, Diatomaceae and also Desmidiaceae are found in abundance. Chlorophyceae and Characeae are rare and are limited to the springs of low temperature. It is not justifiable, therefore, to attribute the thermophylic characteristic to Cyanophyceae only. As far as the degree of thermophily is concerned, the Cyanophyceae and Bacteriae may be placed first. To relate evolution merely to the degree of thermophily would be going too far, and in my opinion this is not at all warranted.

The main argument for the hypothesis that the Cyanophyceae are the oldest inhabitants of the earth is the following: (1) Their apparent low organization; (2) the striking disjunction of several forms through the widely distributed thermal springs of the earth; and (3) the thermophilous character.

If we consider first the degree of organization of the Cyanophyceae, we know today that although their cellular structure shows differences their nature is nevertheless very complex, and has really never been fully analysed. Even at the present time various views concerning their structure are current (Baumgärtner, Cowdry, Prát, Geitler). Whether the Cyanophyceae represent a specialized group or a very reduced developmental type is difficult to determine. It appears that several Cyanophyceae existed in the archaic age (Gruner, Tampelajo), however, these reports are mere assumptions. There seems to be no doubt that the Cyanophyceae do not represent the original organisms from which the remaining plants have developed. Secondly, we must consider the apparent disjunction of several Cyanophyceae. If we take into consideration, for example, the typical form *Mastigocladus laminosus* it seems strange that this alga is found in most thermal regions of the earth and in order to explain this fact, the idea of relict has arisen. According to this view this alga showed at one time a general distribution, but at that time the entire surface of the earth was apparently covered with hot waters. Today the alga is found only in locations very distant one from another, and these are considered "relict stations." My own physiological investigations have taught me that in order to explain the disjunction it is not necessary to resort to the theory of relicts. I have found that *Mastigocladus laminosus* in a resting or latent condition at the usual temperature of the water, or even in the dry condition, is able to exist for months or even years without losing the capacity for active life, growth, and reproduction. This goes far to explain the wide distribution possibility of these algae and it explains also the accidental disjunctions.

If we may consider again the characteristic of thermophily I only wish to add to what has been said by stating that this capacity is also a property of other algae, although to a much smaller degree. If Diatoms, Desmidiaceae, Chlorophyceae, and also Characeae exist at higher temperatures, we consider this an adaptation phenomenon. I find no reason not to affirm this also for the Cyanophyceae. The progress of the Cyanophyceae in the direction of thermophily becomes explainable if we consider the generally known and extraordinarily wide range of this capacity for adaptation in the Cyanophyceae, a capacity exhibited in

respect to many extreme condition of life. The Cyanophyceae and the Bacteria, we may say, are in every respect the most euriphilous organisms.

From what has been shown above I am of the opinion that it would come nearer the truth if I venture to say that the property of thermophily in the Cyanophyceae is of a secondary nature, i. e., *that the entire present thermal vegetation is only an adaptation flora to water of high temperature.* To conclude from previous biological investigations of thermal waters that the thermophilous Cyanophyceae are the first living organisms of the earth is not permissible.

Since these considerations force me to assign to the thermal flora only an adaptive relation, I must also raise the question concerning the time in the history of the earth when this adaptation occurred. In answering this question I believe I am right in assuming that the migration of forms of fresh water algae from cold regions occurred at different times, and this also explains why the thermal flora is composed of such different elements as far as thermotolerance is concerned. It is also possible that certain Cyanophyceae represent the oldest immigrants, but it is impossible to say at what time in the development of the earth this migration occurred, since we have not a single important fact to guide us.

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UEBER ZELL- UND SAMENSTIMULATION[1]

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Von theoretischen Erwägungen ausgehend und gestützt auf frühere Arbeiten von mir und anderen Forschern (Loeb, Delage), habe ich im Jahre 1914 den Gedanken ausgesprochen, dass die Erscheinungen der künstlichen Partheno-genese allgemeine Zellstimulationserscheinungen sind und es folglich möglich sein müsste, durch Einwirkung auf die Zelle mit chemischen und auch physika-lischen Mitteln die Lebensfunktionen derselben zu beschleunigen und zu heben.

Diese Auffassung habe ich durch eine Anzahl von Experimenten an ein- und vielzelligen Tieren bewiesen und diese Art der Hebung der Zellfunktionen als Zellstimulation bezeichnet.

Beim Arbeiten mit Embryonalzellen zeigte sich, dass die Stimulationsein-wirkung nicht eine vorübergehende ist, sondern dass sie sich auf die ganze Periode der individuellen Entwicklung erstreckt.

Von dieser grundlegenden Feststellung ausgehend, habe ich dann, in demsel-ben Jahre, 1914, meine Untersuchungen auch auf pflanzliche Objekte ausgedehnt, und zwar hauptsächlich auf Pflanzensamen, in der Voraussetzung, dass eine Stimulierung der Zellfunktionen derselben — weil diese hier direkt auf embryonale Zellen angewendet wird—eine lang dauernde Wirkung auch auf die nachträgliche Entwicklung der aus den Samen entstehenden Pflanzen haben müsste, und dass man infolgedessen aus den stimulierten Samen Pflanzen ziehen könnte, die eine üppigere individuelle Entwicklung aufweisen und folg-lich auch einen Mehrertrag an der gesamten Trockensubstanz bezw. der Samenernte ergeben würde.

Die seit 12 Jahren unaufhörlich in dieser Richtung von mir gemachten und fortgestzten Versuche—sowohl im Laboratorium als auch auf dem freien Lande—haben meine Voraussetzungen vollständig bestätigt. Es gelang mir, zu beweisen, dass die aus den stimulierten Samen gezüchteten Pflanzen imstande sind, einen Mehrertrag an Ernte hervorzubringen, der sich bei dem gegenwärtigen Stand meiner Untersuchungen durchschnittlich zwischen 20 und 30% bewegt.

Diese Versuche haben mir gezeigt, dass der von mir ausgesprochene und durch theoretische und praktische Arbeiten erhärtete Gedanke einen neuen Weg zur Erhöhung der landwirtschaftlichen Produktion weisen könnte.

Bis jetzt ist die Landwirtschaft zur Erhöhung ihres Ertrages auf folgende Massnahmen angewiesen: (1) Auf die rationelle Bodenbearbeitung, (2) auf die künstliche Düngung, und (3) auf die Methoden der Pflanzenselektion.

Der von mir gezeigte Weg, die bisherigen, in den drei oben genannten Punkten gewonnenen Errungenschaften als gegeben betrachtend, bezweckt, zu einer vierten Möglichkeit der Ertragssteigerung der Kulturpflanzen zu gelangen, indem er die Pflanzenentwicklung durch eine geeignete Stimulationsvorbehandlung der Samen günstig beeinflusst. Ich bin der Ueberzeugung, dass diese vierte Möglichkeit durch weitere theoretische Bearbeitung der Stimulationsfrage und durch Verbesserung meiner Samenstimulationsmethoden sich ebenbürtig den drei vorher erwähnten ertragsteigernden Massnahmen zur Seite stellen wird.

Meine Angaben über die Wirkung und praktische Anwendbarkeit der Stimulation sind im grossen ganzen durch ausgedehnte Landversuche in den Jahren 1923, 1924, 1925, auch in Deutschland bestätigt worden. Zwar kann ich nicht verhehlen, dass sowohl in Bulgarien wie auch in Deutschland ca. 30-40% der angesetzten Versuche negativ, d.h. ohne nennenswerte Steigerung in der Intensität der Pflanzenentwicklung verlaufen sind. Deshalb lautet jetzt die Fragestellung für die weiteren Samenstimulationsarbeiten folgendermassen: die Ursachen festzustellen, welche hinderlich für die günstige Auswirkung der Stimulation mitwirken. Es scheint, dass wir hier vor einen Komplex von Erscheinungen stehen: Wirkung des pH. Gehaltes der Stimulationslösung und des Bodens; Wirkung der Bodenzusammensetzung; Wirkung des Kunstdüngers; Wirkung der klimatischen Bedingungen etc., deren genaue Erforschung im Zusammenhang mit der Frage der Samenstimulation noch bevorsteht.

Welche intimen Prozesse spielen sich nun in der Zelle während eines Stimulationsvorganges ab? Durch langjährige Arbeiten war ich zu der Aufstellung der Hypothese gekommen, dass die stimulierten Zellen eine erhöhte Oxydationstätigkeit aufweisen, und dass wir diesen Zustand der erhöhten Sauerstoffatmung durch eine vorherige, abgemessene und genau dosierte Desoxydationseinwirkung auf die Zelle herbeiführen könnten. Diese Hypothese der desoxydierenden Wirkung der Stimulationsmittel erwies sich von grossem heuristischen Wert und erlaubte mir, eine grosse Zahl von chemischen Mitteln bis jetzt weit über 100—herauszufinden, denen sich auch einige physikalische Mittel anreihen, die ausgesprochene Zellstimulationseigenschaften besitzen.

Mit der Zeit erwies sich aber diese Arbeitshypothese als ungenügend, da es sich herausstellte, dass es chemische Mittel gibt, welche eine desoxydierende Wirkung nicht haben und doch stimulierend wirken.

Die neuerdings von anderer Seite vertretene Ansicht, dass die Stimulationsmittel wahrscheinlich als Koenzyme bei der Hebung der Enzymtätigkeit der Zelle wirken, kann als erschöpfende Erklärung der Zellstimulations-Erscheinungen auch nicht dienen; sie ist ausserdem schwerlich als erfolgreiche Arbeitshypothese zu verwenden. Deshalb habe ich versucht, der Frage der Zellstimulation von der kolloidalchemischen Seite aus näherzukommen (1923). Es zeigte sich nämlich, dass die Stimulationsmittel die Fähigkeit haben, bei bestimmter Konzentration und bei experimentell genau festgestellter Zeit der Einwirkung, den Kolloidzustand der Zelle so zu beeinflussen, dass sie ihre Aufnahmefähigkeit für Wasser erhöht, wodurch die Zellkolloide in optimalen Zustand der Lösung gebracht und folglich auch für die Intensität des integralen

Zellchemismus die optimalen Bedingungen geschaffen werden. Die genaue experimentelle Feststellung der Grenzen der optimalen Einwirkung ist unbedingt notwendig für den positiven Erfolg eines Stimulationsversuches; denn vor dieser optimalen Grenze liegt die Phase einer angehenden Stimulation und nach Ueberschreitung derselben gerät die Zelle in die Phase der Ueberstimulation, welche in ihrer extremen Entwicklung·zur Desaggregation und zum Tode der lebenden Substanz führt.

Die Erscheinungen der Zellstimulation werden in planmässiger Arbeit an einzelligen und vielzelligen Tieren und Pflanzen weiter verfolgt. Ihre genaue Erforschung verspricht wichtige theoretische und praktische Resultate nicht nur auf dem Gebiete der Landwirtschaft, sondern auch auf dem Gebiete der Ernährungs- und Reizphysiologie (a) Berücksichtigung des Einflusses der Zellstimulation auf die Ernährung und (b) Feststellung des Stimulationswertes mancher Nahrungsstoffe und folglich die Erforschung ihrer doppelten Bedeutung für die chemische Metabolie der Zelle, wie auch auf dem Gebiete der Medizin.

PHYSIOLOGICAL INVESTIGATIONS ON ORCHID SEED GERMINATION[1]

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Ever since the work of Bernard ('09) on the relation of the endophytic fungus of the orchid root to seed germination, the orchid with its endophytic fungus has been considered as the classical case of symbiosis among higher plants. Symbiosis means, of course, according to De Bary the living together of two organisms,— whether or not the one is destructive of the other is of no consequence. In the case of the orchid, however, it has been generally accepted until recently that the fungus is of some value to the orchid. With evidence furnished by Bernard for orchids, other investigators have been encouraged to ascribe various functions to those fungi living within or massed about the surface of roots, associations which are termed respectively endotropic and ectotrophic mycorrhiza. Not only has emphasis been placed on either a direct or indirect nutritional relation but Bernard and more recently Magrou have considered symbiosis as an important factor in the evolution of perennial and biennial plants from annuals and both emphasized the idea that the formation of tubers, rhizomes, and bulbs is dependent on a fungous infection of the host plant.

It would constitute an extremely interesting field for research work could these conclusions of Bernard and Magrou be substantiated and the economic phases of this problem might conceivably attain an importance comparable to that found today in the case of leguminous plants and the nitrogen fixing bacteria. It was with some such visions in mind that I began my investigations on orchid seed germination. At the outset I had accepted as a matter of fact the essential conclusions of Bernard in respect to the necessity of the fungus for germination. I was nevertheless impressed with the extreme novelty of the reported physiological relationships of the fungus and orchid embryo and was thus led to a critical study of Bernard's papers and to a reinvestigation of the problem. Whatever expectations I had in respect to the necessity of symbiosis for germination of orchid seeds were greatly lowered by a critical reading of the investigations of Bernard and Burgeff. Great credit is due Bernard for the excellence of much of his work but the deductions made by him relative to the necessity of the fungus for germination are not warranted by the experimental evidence.

Before we consider in a critical manner some of the contributions of Bernard ('09), Burgeff ('09), and others let us hastily consider some of the characteristics of orchid seed. These seed are minute. A *Cattleya* seed is only about 150μ in

length and 90μ in breadth and seed of various other genera are even smaller. The embryo is enclosed within a transparent membrane open at the end. The embryo is undifferentiated except that the basal cells are somewhat larger than the cells of the meristem. Cotyledons are not differentiated. There are no tissues for reserve food. The food present in the embryo of *Cymbidium* is largely fat, which constitutes 32% of the dry weight, according to our analyses. Sugar is about 1% and there is no starch.

The mode of germination is unusual. The minute embryo of *Cattleya* or *Odontoglossum* when placed under favorable conditions immediately begins to absorb water, swelling takes place, and evidence of enlargement is visible with a hand lens in eight hours. Within ten days and sometimes even within four days chlorophyll or a related pigment appears. The seed assumes a spherical shape. Absorbing hairs push out as extensions of epidermal cells and later a few stomates may appear at the apical portion of the embryo. A leaf point appears, and the extension of the meristem gives rise to the stem, from which the first root appears. The enlarged corm or basal portion is termed the protocorm. We now have a seedling. This development may take from four weeks to ten weeks depending upon the conditions and species. With *Cymbidium*, *Vanda*, and seed of some other genera, the developing embryo is without chlorophyll for the first four weeks or longer.

All of these facts, the slow germination, the lack of reserve food, the small size, etc. make the seed especially liable to destruction by plant and animal organisms as well as by other unfavorable environmental conditions. Fifteen months ago I sowed more than 200,000 seed of *Oncidium* sp. on a *Croton* plant in Guatemala, on which plant the parent itself was growing and after six months I could find only two tiny seedlings. But ignoring entirely the matter of environmental factors, we find inherent characteristics that compel us to admit that germination is possible only under rather unusual circumstances. Whatever view finally prevails it must be admitted that the problem of orchid seed germination is not only one of interest but one involving problems of fundamental significance.

When Bernard began his work about twenty-five years ago practically nothing was known about the germination of orchid seed. Now and then some grower hit upon the right conditions for germination but failure was more common than success, and considering the germination of the seed of various genera this still holds true except where pure culture methods are used. Bernard was impressed by his observations that a practice often yielding successful germination was to sow the seed on the substratum about the parent plant. He had noted that the embryos were infected with a fungus and conceived the idea that the fungus found in the orchid root was necessary for germination.

This then became his starting point. He proposed to isolate the endophytic fungus, to determine if the seed would germinate under aseptic conditions in the absence of the fungus, and to compare the behavior of infected and non-infected seed. Seed were obtained aseptically from ripe capsules and sown immediately in culture tubes, the nutrient solution being a decoction of salep to which agar was added. Salep is made by pulverizing the tubers of a species of

Ophrys and it contains pentosans, starch, and a small amount of sugar and proteins, as well as other substances. Most of the food present is in an insoluble form. This is a fact of great significance in the interpretation of Bernard's results. Bernard made a large number of experiments using seed of plants of various genera and studied the relation of the different orchid fungi to germination. The basic facts which Bernard offered to sustain the theory of obligative symbiosis for orchids may be summarized in the following statements. (1) Orchid seed will not germinate under pure culture conditions on a nutrient medium containing a relatively low concentration of salep. If, however, the appropriate orchid fungus is applied, then germination may take place. Many of the embryos may be killed by the fungus but those that germinate have the basal portion of the embryo infected. (2) Bernard isolated three different fungi, all of which he described as species of *Rhizoctonia*. Any one of the three fungi was only effective in inducing germination of seed of those orchids in which the particular fungus was normally present. (3) There appeared to be essential for germination a delicate balance between the host and the extent of development of the fungus. Too pronounced a growth of the invading fungus resulted in death. Too little growth of the infecting fungus resulted in no germination. (4) The constancy of association of fungus and orchid was considered as significant of an essential relationship. With certain minor exceptions the work of Burgeff seemed to confirm the work of Bernard.

Aside from the fact that on a salep or starch nutrient medium there would be no germination without the appropriate fungus, the most striking evidence in favor of obligative symbiosis was the behavior of seed of *Phalaenopsis*, to the fungi isolated respectively from *Phalaenopsis*, *Cattleya*, and *Odontoglossum*. These fungi represent the three distinct species reported by Bernard. With the fungus from *Phalaenopsis* the seed of *Phalaenopsis* germinated, but with the fungus from *Cattleya* the *Phalaenopsis* embryos were killed because of too intense an infection. With the fungus from *Odontoglossum* there was no germination of the seed of *Phalaenopsis* because according to Bernard the digestion of the fungus by the host was too excessive. The explanation for the failure of germination with the fungus from *Cattleya* is perfectly clear. The fungus proved to be a strong pathogen. With the fungus from *Odontoglossum* I believe that no germination was possible in the time because of the fact that the fungus from *Odontoglossum* is a more prolific grower than that of *Phalaenopsis* and growth of the orchid embryo was retarded because of failure in the competition with the fungus for food in the culture medium. Such results may be paralleled with seed of *Cattleya* using only the *Cattleya* fungus and varying slightly the nutrient conditions.

In attempting to explain the action of the fungus, Bernard made use of an experiment which should have given him the real clue. He found that the fungus could invert cane sugar in a nutrient solution. This, of course, increased the osmotic concentration. Therefore the action of the fungus according to Bernard was to change starch within the embryo to sugar. This increased the concentration within the cells and acted as a physical-chemical stimulus to growth.

He compared the action of the fungus to the action of a male gamete in fertilization.

Bernard was the first to germinate seeds by the non-symbiotic method. He used high concentrations of salep (which contained therefore higher quantities of soluble sugars, etc.) and obtained germination of seeds which he described as normal. But the explanation given was that the high concentration used was equivalent to a physical chemical stimulus comparable to artificial fertilization of an egg by chemical methods. He ignored entirely the food relationships.

Burgeff noted results similar to Bernard's when using starch in the culture medium. He concluded that the fungus changed the starch in the embryos and this sugar was used in growth.

Let us now consider these deductions of Bernard and Burgeff in the light of my own investigations ('22, '24, '25), on the germination of orchid seed. When a nutrient medium is used containing only the essential salts and agar there is no germination. The seeds of *Cattleya* and those of certain other genera begin to grow and develop a green color. After about two months growth ceases and despite the apparent presence of chlorophyll no further growth is made. Such embryos I have maintained alive in tubes for two years. When these embryos are transferred to another culture tube containing a nutrient medium with either glucose, fructose, or sucrose, then growth of the embryos is resumed and a seedling is soon produced. That this is due to a food relationship and not to any osmotic effects as stated by Bernard must be apparent from the fact that lactose is without any effect and the same is true for certain other sugars that cannot be assimilated.

In a great many experiments with seed of *Cattleya, Laelia, Vanda, Oncidium, Odontoglossum, Cymbidium, Dendrobium, Epidendron, Cypripedium, Ophrys* and with seed of plants of other genera no germination has resulted when only the essential salts and water were provided. Working under my direction, Dr. Ralph Nanz has attempted to stimulate germination on a mineral nutrient medium by wounding, etherization, and by other methods but thus far without any success. These facts are of great significance in indicating that the embryos of orchids are saprophytes and must have organic food supplied until the photosynthetic processes are self-sufficient for the plant.

In the case of *Cattleya* seeds, the embryos may be grown with sugars for about one month and then removed to a nutrient medium lacking sugar. The embryo will then continue to develop without a supply of sugar and without the fungus. I have plants of this character five years old that have been grown entirely within flasks which plants are about as good as the usual five-year-old plant. These particular plants of *Cattleya* were saprophytic then only during the first month of germination.

Those who are proponents of the symbiotic view state that the sugar in this case is merely a substitute for the fungus and that in nature no sugar is present. Bernard himself found germination possible with high concentrations of salep, but considered the high concentration as merely a physical chemical stimulus to the embryo. But so impressed were Bernard and Burgeff with the necessity

of infection that they ignored entirely the possible effect of the fungus on the organic matter of the nutrient medium. I stated in my first paper that probably germination with the fungus was due not to infection of the embryo but to the transformation of insoluble organic food in the culture medium to soluble foods and these with products excreted by the fungus were responsible for germination.

In order to test this hypothesis a fungus from *Cattleya* sp. was isolated and this organism seemed to fit the description given by Bernard. Preliminary trials showed it to be capable of bringing about germination when the culture medium contained starch. Examination of the seedlings showed characteristic infection. It seemed permissable to conclude that we were working with the correct organism.

Various experiments were then made to determine whether or not the effect of the organism on germination could be explained on the basis of the effect of the fungus within the embryo or upon the organic matter of the culture medium. Whenever the culture medium was inoculated with the fungus the starch present was soon changed to sugar and the hydrogen ion of the culture medium altered from pH 6.0 or pH 5.5 to about pH 4.7. Here then was evidence that external changes occurred and these changes were sufficient to explain germination without postulating an internal effect of the fungus. It was found that the higher the initial starch content of the culture medium, the higher was the sugar content and the more rapid the growth in inoculated cultures. These data are shown in table 1 and the cultures in figure 1. But of equal significance is the fact that the embryos that germinated in the inoculated tubes with 2 per cent starch were
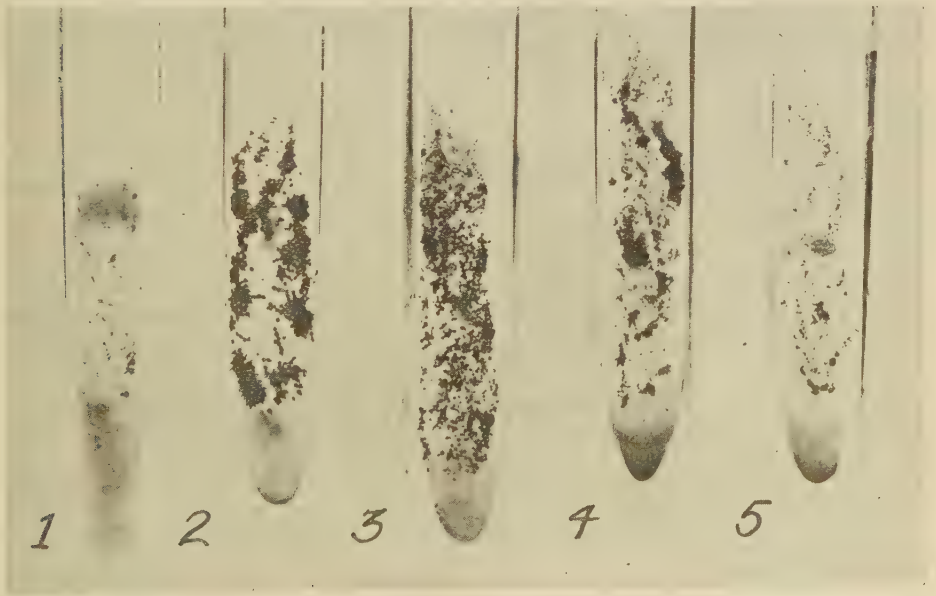
Fig. 1. Control culture, ¼% starch. Not inoculated; (2) 2% starch, inoculated; (3) 1% starch, inoculated; (4) ½% starch, inoculated; (5) ¼% starch, inoculated.

entirely free of infection.   The infection of the embryo became greater with decrease in starch content and the percentage of embryos killed by the fungus increased the lower the initial starch content of the culture medium.   Certainly in these experiments the evidence is clear that the action of the fungus is external.

TABLE 1. CATTLEYA HYBRID SEEDS PLANTED NOVEMBER, 10, 1923: NOTES MADE JANUARY 10, 1924

Culture sol.	Inoculation	Culture No.	Ave. width of embryos (μ)	Max. width of embryos (μ)	pH of cult. medium	Glucose per cult. tube (mg.)
B+$\frac{1}{4}$% starch	Dec. 11	SL 2	211	291	4.7	5.9
B+$\frac{1}{4}$% starch	None	SM 7	124	144	5.5	0.0
B+$\frac{1}{2}$% starch	Dec. 11	SM 1	268	384	4.7	28.7
B+1% starch	Dec. 11	SN 1	311	480	4.7	63.8
B+2% starch	Dec. 11	SO 2	393	576	4.7	121.8
B+2% starch	None	SO 7	124	144	5.5	0.0

In certain experiments not yet reported it was noted that arabinose sugar could not be utilized by the orchid embryo.   The orchid fungus however would grow with this sugar and despite infection the embryos did not germinate.   In my third paper I also presented evidence to show that embryos adhering to the wall of the culture tube and infected did not germinate and in fact measured only 198μ in diameter while the embryos on the starch medium not inoculated were 225μ in diameter.   In the case of the embryos on the wall, hyphae extended from embryos to the culture medium.

These and other experiments suggest that any fungus which could digest starch and produce the proper reaction in the culture medium would induce germination.   A number of organisms were tested and some embryos germinated in every tube but for the most part the growth of the fungi was too great and "smothered" the embryos.   One organism *Phytophthora* sp. isolated by Prof. H. H. Whetzel from Easter Lily (*Lilium* sp.) was about as effective as the orchid fungus, but of course the embryos were not infected.

In another experiment germination of the embryos occurred on a mixture of osmunda fiber and sphagnum to which had been added nutrient salts, and the reaction maintained at pH 4.9.   The orchid fungus was lacking in this culture but soluble organic food was derived by the orchids from the organic matter present.   An infection by *Penicillium* in another culture accelerated the rate of growth of the embryos and this was correlated with an increased quantity of reducing sugars.

One of the points made by the proponents of obligative symbiosis is that the fungus from *Odontoglossum* is not effective for *Cattleya* nor is the fungus from *Phalaenopsis* of value for *Odontoglossum*, etc.   In certain experiments I found that the fungus from *Cattleya* killed the seed of *Odontoglossum* and similar results were reported by Bernard.   This of course, suggests merely the pathogenic character of the organism for a particular host.

If we are to dismiss the idea of obligative symbiosis as a condition for normal germination how can we explain the striking behavior of orchid seeds in their failure to germinate when provided with the essential salts, water and other

favorable environmental conditions. In the embryos of various genera of orchids cholorophyll is apparently produced within the first ten days, yet the embryos cease growth within a short period of time. Either the amount of food synthesized is just equal to that consumed in maintaining life or we have a case of delayed photosynthesis as reported by Briggs ('20) and others. This assumes that there is lacking some internal factor necessary for the process of photosynthesis. The embryos of other orchid genera, for example, *Cymbidium*, *Vanda*, *Ophrys*, *Epipactis* and others are without chlorophyll for the first five or six weeks or longer. They are saprophytes and must obtain soluble food from the substratum on which they are growing. Despite the presence of chlorophyll it must be concluded that in the early period of life those embryos that appear to possess chlorophyll are also saprophytic. Growth of these can take place only when organic food is available. This saprophytic character is only temporary for even before the leaf point appears the embryo may be transferred to a culture solution containing only the nutrient salts and water. The orchid is thereafter autotrophic.

The criticism is made that in nature sugar at concentrations comparable to those used in culture media is never available. The concentration available is of no great consequence. In certain experiments on plant extracts the sugar concentration was less than 0.02 per cent, yet germination took place. The capacity of the plant to remove minute traces of solute is well established. In nature the orchid embryos are found in a substratum high in organic matter. Here a variety of microoganisms bring about the transformations of the insoluble organic matter to the soluble forms and while the concentration may be low the supply is constant. It is furthermore pure assumption to conclude that the orchid fungus and no other organisms are involved in the transformations of the insoluble organic substances to the soluble forms.

In conclusion it is my opinion that the unusual requirements of orchid embryos for germination may be explained on the inability of these plants to synthesize food. They are therefore purely saprophytic in early life and must obtain organic food from the substratum. The fungus is a pathogen held in check, or not, depending on the physiological condition of the host. The constancy of association of fungus and orchid merely signifies to me that the orchid fungi are as widely distributed as the orchid plants. There is no reason for assuming a significant relationship other than mild parasitism.

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ON A NEW CONCEPTION OF THE CONSTITUTION OF PROTEINS[1]

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The elucidation of chemical and physical properties of protoplasm, the material basis of life phenomena, forms one of the fundamental problems of biology. Our science might be proud of the fact that almost all essential knowledge concerning the chemical composition of protoplasm has been derived from the elaborate studies of botanists, Reinke and Rodewald, and more recently Lepeschkin, Iwanoff, and Kiesel, on myxomycetous plasmodiums. As the result of these investigations, the greatest significance among the constituents of colloidal protoplasmic matter must be assigned to proteins, which in themselves or in various combinations with lipoids, nucleic acids, or carbohydrates, are concerned undoubtedly in all phases of metabolic activities of living cells. The specificity of living matter, underlying the mechanism of heredity and evolution in diverse organisms, can only be explained on the ground of structural variations possibly displayed by no other compound than proteins. In fact, the protein problem attracted for a long time the active attention of both physiologists and chemists and continues to occupy a central position in biochemical research.

As to the chemical constitution of proteins, full recognition was given for a long period of time to the polypeptid theory of Emil Fischer. The founder of this theory conceived that the gigantic molecules of proteins consist essentially of several amino acids joined together by means of the so-called peptid linking,–CO–NH–, thus forming a long chain. As early as 1907 E. Fischer synthesized an eighteen-membered polypeptid from glycocoll and leucin, certain characters of which resembled those of proteins, so that the author contented himself with being able to push forward his synthetic work in the group of true proteins by merely adding some two or more amino acids to the chain.

In recent years, however, different points of view on this subject were introduced by a number of investigators. According to them, the molecules of amino acid anhydrides, which are mostly derivatives of diketo-piperazines, are bound together by a force of other than that of ordinary valency, giving rise in the aggregate to a colloid-micell of definite magnitude, that is, the so-called "molecule" of proteins.

Apparently this new idea occurred to the minds of investigators through an analogy with the now prevalent and well-founded conception of the constitution of polysaccharides, such as cellulose, starch, glycogen, inulin, etc. These poly-

saccharides are regarded as association or polymerization products of the so-called "ground bodies", that is, anhydrides of simple sugars.

The theory of the anhydridic structure of protein is now receiving strong support from many sides. I shall mention some of the outstanding evidence from recent experiments:
(a) Its characteristic color reaction towards alkaline solution of picric acid; (b) its oxidation and reduction products (Abderhalden); (c) its röntgenographic studies and the determinations of its molecular weight (Herzog); (d) the action of hypobromite on it (Goldschmidt); and (e) its racemization in alkaline media (Levene).

I have myself undertaken an extended research in this field and I published some preliminary notes last year.[2] My first attempt was to depolymerize certain proteins into their ground or basal constituents by adapting a method from polysaccharide chemistry, which procedure was originally devised and accomplished by Pictet and H. Pringsheim, and has proved most satisfactory. I found when various proteins were heated with a quantity of anhydrous glycerin for a few hours at about 180° C., and the resulting brown-colored solution extracted with choroform, ether, or other suitable organic solvent, a good yield of crystalline residue was always obtained. This substance manifested the characteristic properties of diketo-piperazines. Even the inert scleroproteins of silk, hair feather, horn, carapace, etc. go into complete resolution after some time.[3]

As the above method does not involve conditions bringing about the hydrolysis of supposed polypeptid chains, any secondary formation of amino acid anhydrides cannot occur, and the original existence of diketopiperazines as the ground substances of proteins would appear more probable than ever.

It would seem that polymerization (association) and depolymerization (dissociation) constitute a reversible process, which proceeds in either direction according to the concentration of starting materials, temperature, and other factors. The next step in the investigation was, therefore, to find out the condition suitable to aggregate diketopiperazines into protein-like complex bodies. The experiments were carried out with free amino acids and amino acid anhydrides. As has already been shown by Maillard, the former can be easily transformed into the latter by heating in glycerin. It was found at the outset that the artificially polymerized anhydrides can be very conveniently isolated as certain metallic compounds. To quote an example from these experiments: Glycin, alanin, leucin, tyrosin, and tryptophane were mixed in their molecular proportion with five molecules of asparagin and heated with less than five parts of glycerin at about 170° C. until a dark brown pasty mass resulted. The latter was dissolved in ten volumes of methyl alcohol and barium hydroxide, or calcium chloride, added. The resultant voluminous flocculent precipitate was sucked up, washed with absolute alcohol and dried in vacuum. The more or less hygroscopic amorphous powder thus obtained, though containing ash, resembles de-

[2] Acta Phytochimica 2: 39. 1925; Bull. Chem. Soc. Japan 1: 19. 1925.

[3] More recently Grenacher has obtained similar results by heating proteins with alcohol in an autoclave. (Helv. chim. acta 8: 784. 1925.)

natured proteins in many respects. It is easily soluble in water, not readily dialyzable, gives all essential color reactions of proteins, namely, Biuret, Millon's, xanthoproteic, Adamkiewicz's, Neubaur-Rhode's, and Voissnet's reaction. It is precipitated from the watery solution by silver nitrate, lead acetate, and other heavy metallic salts, and also by acidified tannic acid solution, and is flocculated by saturating with ammonium sulphate. It contains no trace of free amino acids, but gives a strong anhydride reaction with soda-alkali, picric acid, or dinitrobenzoic acid solution.

Although the nature of anhydrides or diketo-piperazines formed and contained in these artificial complex aggregates is not to be easily elucidated, similar experiments have been conducted with both a single amino acid and a couple of two distinct amino acids, giving rise to diketo-piperazines of known constitutions, which might be expected to throw light upon the exact mode of polymerization. Now, for example, if we heat asparagin with 3–4 parts of glycerin at 160 –170° C. for an hour, three different anhydrides or their tautomeric forms are found to be present in the resulting brown pasty mixture, the free acid amide group being thereby partially hydrolyzed by the action of unavoidable moisture; these anhydrides being:

(1) $$NH_2 \cdot CO \cdot CH_2 \cdot CH. CO \cdot NH$$
$$\dot{N}H. CO \cdot \tilde{C}H_2 \cdot CO \cdot NH_2.$$
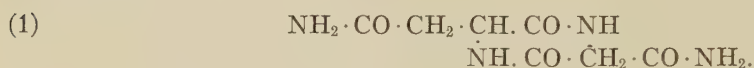
Diketo-piperazine diacetic acid di-amide. (Asparagine amide)

(2) $$NH_2 \cdot CO \cdot CH_2 \cdot CH \cdot CO \cdot NH$$
$$\dot{N}H. CO \cdot \dot{C}H \cdot CH_2 \cdot COOH.$$
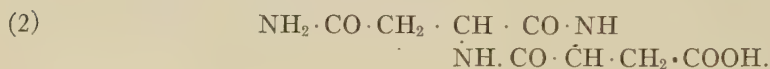
Diketo-piperazine diacetic acid mono-amide.

(3) $$HOOC \cdot CH_2 \cdot CH. CO \cdot NH$$
$$\dot{N}H. CO \cdot \dot{C}H \cdot CH_2 \cdot COOH.$$
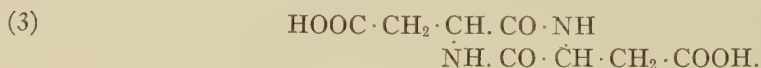
Diketo-piperazine diacetic acid.

The tautomeric forms of diketo-piperazine nucleus being either

$$-C = \dot{C} \cdot NH \qquad \text{or} \qquad H\dot{C} - \dot{C} = N$$
$$\dot{N}H \cdot C = \dot{C}- \qquad\qquad \dot{N} = C - \dot{C}H$$

with OH groups as shown.
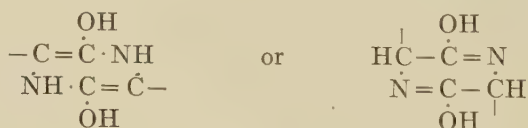
From alcoholic solutions of the pasty mass above mentioned, a copious amorphous precipitate is thrown down on addition of either neutral salts or hydroxides of alkaline earth or many other metals. The precipitate, when dried in vacuum, forms a light-colored powder, the yield amounting usually to not less than 50 per cent of the amino acid used. The analysis and kryoscopic molecular weight determinations indicate a dimeric nature of the substance, that is, a polymeride of either two molecules of the anhydrides above given, combined with one atom of a bivalent metal, which anhydrides are named "aspartans" for the sake of brevity.

By eliminating the metals from the watery solution of the above-mentioned substance by the usual methods, we obtain a highly associated di-aspartan, free of ash, which displays many remarkable colloidal behaviors. This substance can be totally hydrolyzed into aspartic acid by treating with boiling 20 per cent hydrochloric acid for many hours. Also, after standing for some days in a half-normal baryta solution, the polymerized aspartans are converted into a dipeptide, aspartyl-aspartic acid, once described by Emil Fischer.[4]

The aspartans seem to be easily hydrolyzed by fungal enzymes, as di-aspartan serves as an excellent nutrient for *Aspergillus* and *Penicillium*.

With the exception of the free diacetic acid form (III), the aspartans, either single or polymerized, show a beautiful biuret reaction. The biuret reaction of natural proteins, which was long assumed to prove Fischer's polypeptide theory may now be accounted for by the pre-existence of certain anhydridic structures, which contain asparagin or glutamin as their component. Further evidence as to the above might be deduced from the fact that various proteins, such as casein, serum albumin, fibrin, gliadin, treated with boiling 20 per cent hydrochloric or sulphuric acid for one or two hours, give off almost all of their ammonia, which originates, as already pointed out by Osborne and others, from free acid amide groups of asparagin or glutamin components in the protein. As we have observed, the biuret reaction becomes thereby lost, though, in this short period of hydroysis, the greater part of the peptide linking should remain intact.

So far as the artificial production of simpler colloidal polymerides of diketopiperazines is concerned, my experiments fall on somewhat the same line with those of M. Bergmann,[5] though utterly different in the methods used. Bergmann recently announced that the synthetic methylene diketo-piperazines form polymerides, which are quite insoluble in water and other solvents, and thus simulate a keratinic type of protein rather than a water soluble one. The polymerides of Bergmann were found, though highly associated in the solid state, to be dimeric by the molecular weight determination in boiling phenol. It is interesting to note that according to Troensegaard and Herzog some typical proteins, gelatin, gliadin, and fibroin, yield in phenolic media values not far exceeding those of dimeric diketopiperazines.

With such simple artificial models at hand, I hope, through further investigations, that a certain insight into the vexed and intricate structure of natural proteins will be gradually gained, and the physiological production and transformation of protein materials in living cells will find their adequate chemical interpretation, and that such a rigid structural conception as gigantic polypeptide molecules will no longer be valid.

[4] Fischer, E. Unters. üb. Aminosäuren, etc., II, 1907–1919. 404.
[5] Ann. d. Chemie 445:1. 1925; 152:189. 1926; 448: 38. 1925.

PFLANZENPATHOLOGIE ALS WISSENSCHAFT
UND UNTERRICHTSGEGENSTAND[1]

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Wenn wir das Arbeitsgebiet der Pflanzenpathologie, wie es bei der Aus-
bildung für den Beruf gelehrt werden soll, umgrenzen wollen, so müssen wir uns
zuerst über den Begriff Pflanzenpathologie klar werden. Denn es ist bekannt,
dass man darunter in verschiedenen Ländern nicht dasselbe versteht. Die
englisch redenden Völker z.B. und Frankreich meinen damit nur den botani-
schen, im wesentlichen mykologischen Teil der Pflanzenschutzforschung, im
Gegensatz zum entomologischen Teil, während man besonders in Deutschland
und Holland die gesammte Lehre von den Pflanzenkrankheiten damit zusam-
menfasst. Der Unterschied scheint sich in der Hauptsache aus historischen
Gründen herausgebildet zu haben. Die angewandte Entomologie hatte in jenen
Ländern schon eine hohe und selbstständige Entwicklung erreicht, als die plan-
mässige Erforschung der Pflanzenschäden im Interesse der Steigerung und Sich-
erung der Pflanzenproduktion eingeleitet wurde. So fanden denn die Botaniker
keinen Anlass, sich über die neu entstandene Mykologie hinaus zu betätigen,
und beschränkten ihre pflanzenpathologische Arbeit auf diejenigen Zustände,
bei denen die Reaktion der Pflanze, die eigentliche Krankheit, im Vordergrund
stand. Damit ist auch schon neben dem äusseren oder geschichtlichen Grunde
ein sachlicher Unterschied gegeben, der sich in der Gegenüberstellung *Krank-
heiten* und *Beschädigungen* (diseases and pests) erhalten hat, wobei man die
tierischen Schäden nicht als Krankheit anerkennt, und der praktisch nie ganz
aufgehoben werden kann. Auf einem Sondergebiet, demjenigen des Forstwesens,
hat sich in Deutschland dieselbe Entwicklung vollzogen. Einer seit langem
bestehenden und hochentwickelten Forstentomologie gegenüber entstand selbst-
ständig eine forstliche Mykologie und nur in der praktischen Anwendung, in der
Lehre von Forstschutz, finden wir beide vereinigt.

Ich bin aber der Meinung, dass die Zusammenfassung der beiden Arbeits-
gebiete zu einer höheren Einheit bei aller getrennten Behandlung der Einzelfra-
gen durch Spezialisten eine notwendige und selbstverständliche Forderung ist.
Und zwar aus theoretischen und praktischen Gründen. Auf den Namen kommt
es dabei nicht an; wir haben im Deutschen dafür den allgemeinen Ausdruck
Pflanzenschutz; er ist in seiner Beziehung auf die praktische Anwendung jetzt
in vielen Sprachen in Übersetzung vorhanden und wir können dabei noch gegen-
über dem praktischen *Pflanzenschutzdienst* die theoretische Pflanzenschutz-

forschung besonders betonen. Auch in anderen Sprachen mag man ein entsprechendes Wort wählen, wenn die Bezeichnung Pathologie zu eng festgelegt zu sein scheint. So strebt man jetzt in Italien an, eine allgemeine Pathologie als "Patologia vegetale" gegenüber den beiden Zweigen der Fitopatologia und der Entomologia agraria aufzustellen (Petri, L. Bollett. d. R. Staz. di Patol. veget. N. S. **6**: 1926 [p.3]). Auch in den Vereinigten Staaten strebt man seit Jahren eine engere Fühlung zwischen beiden Richtungen und Vertiefung der gemeinsamen Grundlagen an (Exp. Stat. Record **44**: 1921 [p.101]).

Auf die praktischen Gründe brauche ich nicht näher einzugehen. Sie liegen auf der Hand, wenn man sich z.B. die kombinierte chemische Schädlingsbekämpfung mit Fungiziden und Insektiziden, die Bodendesinfektion gegen Bakterien, Pilze und Insekten, die besondere Einstellung von Kulturmassnahmen auf die Prophylaxe von Krankheiten vergegenwärtigt. Der so oft gebrauchte Vergleich mit der Human- und Veterinär- Medizin trifft hier vollständig zu. Es wird auf die Dauer weder die Beratung des Pflanzenbauers im einzelnen Fall, noch das staatliche Eingreifen in Gesetzgebung, Einfuhrkontrolle und Quarantäne eine doppelte, nebeneinander laufende Behandlung der Pflanzenschutzfragen ertragen. Die Trennung kann erst da einsetzen, wo die Arbeit des Spezialisten notwendig wird. So haben denn auch die neueren Pflanzenschutzgesetze in allen Ländern, ebenso auch staatliche Institute sowie manche Vereinigungen von Forschern und Publikations- organe diese Konsequenz gezogen. Noch wichtiger scheinen mir aber im Interesse der Förderung des Pflanzenschutzes die theoretischen Gründe. Die heutige Entwicklung der Forschung drängt geradezu darauf hin. Die einseitig zoologische oder mykologische Arbeitsrichtung wird den Grezgebieten nicht gerecht und lässt andere ganz ausser Acht. Solche Grenzgebiete sind ausser den genannten praktischen die mit der Pflanzenzüchtung zusammenhängenden Fragen der Anfälligkeit und Immunität der Pflanze, der Spezialisierung, Virulenz und des Wirtswechsels der Parasiten, die Übertragung von bakteriellen und Virus-Krankheiten durch Insekten, die Bekämpfung dieser Insekten, die biologische Bekämpfung von Insekten durch Bakteriosen und Mykosen, von Unkräutern durch parasitische Insekten.

Aber auch die eigentliche Krankheitslehre oder Pathologie der Pflanzen kann nur gefördert werden, wenn sie sich von ätiologischer Bindung loslöst. Hier liegen grosse Aufgaben, auf die noch wiederholt hinzuweisen sein wird.

Die Durcharbeitung des Systems einer allgemeinen Pathologie der Pflanzen, die einheitliche Bearbeitung der ökologischen Probleme, die Fragen der Giftwirkung der Parasiten und der Immunitätsreaktion von Pflanzen, die Entstehung der Gallen und Tumore und die Bearbeitung der nichtparasitären Krankheiten überhaupt sind solche Probleme, die eine zentrale, zusammenfassende Behandlung verlangen.

Nicht zuletzt liegt diese im Interesse des Unterrichts, genauer gesagt, der Ausbildung des Pflanzenpathologen. Hier ist die allgemeine Pathologie als Grundlage notwendig, um den Spezialisten der einzelnen Forschungsrichtung einen zentralen Überblick über Gesamtgebiet und eine Kenntnis der prinzipiellen biologischen Fragen zu übermitteln.

Für den Unterricht in Forschung und Praxis sei noch auf die Bedeutung der Symptomatik hingewiesen, deren Aufgabe es ist, zu zeigen, in welcher Weise die Pflanze auf schädliche Einwirkungen reagiert. Das Fehlen einer solchen Betrachtungsweise hat gerade bei der Feststellung der Erreger oft zu Schwierigkeiten und Fehlern geführt, indem man aus Krankheitserscheinungen auf bestimmte Gruppen von Erregern schloss, ohne sich bewusst zu sein, dass sie vielfach spezifische Reaktionen der Pflanze, nicht aber die Wirkung spezifischer Reize des Erregers darstellen. Solche Fälle sind jetzt allgemein bekannt; die Rötung vieler Gramineen, das Welken, Blattrollen, wie überhaupt die Nekrosen, aber auch Verkümmerungen, andererseits Knospensucht und Hexenbesen und das ganze Kapitel der Gallenbildung gehören hierher.

Auf viele der oben erwähnten Einzelheiten wird noch zurückzukommen sein.

Es ergibt sich, dass die Pflanzenpathologie, ob man ihr Dasein nun von den Bedürfnissen der praktischen Landwirtschaft oder vom Arbeitsfeld der angewandten Botanik ableitet, in ihrer Durchdringung von botanischen und zoologischen Fragen ein selbständiges biologisches Gebiet darstellen muss, das wohl in einzelne Arbeitsrichtungen zerfällt, aber seine Einheit in der Erforschung der pathologischen Vorgänge der Pflanzen findet.

So muss sich die Pflanzenpathologie über den bisherigen Arbeitsrichtungen synthetisch als eine eigene Wissenschaft aufbauen. Das mag manchem ungewohnt erscheinen, da die Wissenschaften umgekehrt den Weg der Spezialisierung gehen und einzelne ihrer Zweige selbständig werden.

Man kann hier an die Entwicklung der Bakteriologie als Beispiel erinnern und es ist in diesem Zusammenhang interessant zu vergleichen, dass die Medizin den Weg immer weitergehender Spezialisation durchgemacht hat. Aus ihr ist neuere Naturwissenschaft zum grossen Teil hervorgegangen. Die weitgehende Spezialisierung ist erst eine Folge der ungeheuren Zunahme des Wissensstoffes.

Noch Linné war bekanntlich Botaniker und Zoologe und noch vor hundert Jahren kam es an deutschen Universitäten vor, dass ein Professor gleichzeitig Botanik und Zoologie vortrug, trotzdem jene scharfe Trennung beider Gebiete bestand, die erst durch das Auftauchen der Biologie als einer synthetischen selbständigen Wissenschaft in der Theorie beseitigt wurde. Auch die Pflanzenpathologie ist heutzutage nichts anderes als angewandte Biologie, wie es schliesslich die Medizin auch ist, die man ja nicht als angewandte Zoologie bezeichnet.

Von der hiermit, wie ich glaube, genügend begründeten Einheit der Pflanzenpathologie als Wissenschaft ausgehend ergibt sich nun die Aufgabe, dieses Gebiet zu umschreiben und einzuteilen, und es kann am besten an einer Einteilung des Unterrichts gezeigt werden, wie sich nun die einzelnen Arbeitsrichtungen der Pathologie im Zusammenhang des Ganzen verhalten. Ich möchte daher in Form eines Unterrichtsprogrammes oder genauer gesagt, eines Programmes für die Ausbildung der Pflanzenpathologen diese Aufgabe beleuchten.

Ich spreche hier von einem theoretischen Programm für die Zukunft, das, ohne auf die so verschiedenen Verhältnisse der einzelnen Länder einzugehen, der Diskussion offen steht, und möchte damit Unterricht und Berufsausbildung zusammenfassen. Denn der Unterricht ist heutzutage vielfach, wie z.B. in

Deutschland, eigentlich nur praktischer oder Fachschulunterricht in Schäd-
lingskunde und Schädlingsbekämpfung, während sich die Ausbildung der Patho-
logen, auch wo sie auf hoher Stufe steht, soviel ich sehe, auf Spezialausbildung
in der angewandt botanischen oder entomologischen Seite beschränkt. Die An-
fänge der allgemeinen Pathologie gehen dabei, wo sie vorhanden sind, von der
Mykologie aus.

Als Berufsstudium ist die Ausbildung in 2 Stufen wie bei anderen wissen-
schaftlichen Berufen zu gliedern, das *Vorstudium* und das *Fachstudium.*

Das *Vorstudium* oder grundlegende naturwissenschaftliche Studium braucht
uns hier wenig zu beschäftigen. Die Hauptsache ist hier in diesem Stadium die
Botanik, und es ist auffallend, wie die eingehende Beschäftigung mit der Pflan-
zenanatomie als Schulung im exakten Arbeiten und Beobachten auch für die
anderen Zweige z.B. die Physiologie die beste Grundlage bildet. An die allge-
meine Botanik schliessen sich dann spezielle Vorlesungen und Übungen in Myko-
logie und Bakteriologie an. Daneben wird allgemeine Zoologie gelehrt, an die
sich als Sonderfach Entomologie anschliesst. Diese beschreibenden Naturwissen-
schaften können durch allgemeine biologische Vorlesungen ergänzt werden. Auf
der Seite der exakten Naturwissenschaften ist eine Einführung in Chemie und
Physik notwendig, die auch wieder durch Vorlesungen und praktische Übun-
gen erfolgt.

Das *Fachstudium* hat dann die eigentliche Ausbildung für den Beruf zu ver-
mitteln, und ich möchte den Hauptwert darauf legen, dass es in seinem Anfang
noch einheitlich auf die Pflanzenpathologie als Ganzes gerechtet ist und erst im
weiteren Verlauf zur Spezialisierung führt. Es muss also den umgekehrten Weg
gehen, den der heutige Pflanzenpathologe durchmacht, der von einem Spezial-
gebiet ausgehend sich sein allgemeines Wissen aufbauen muss.

Der Lehrgang muss daher drei gleichwertige Teile umfassen:
1) *Allgemeine Pflanzenpathologie,* an welche die nichtparasitären Krankheiten
und eine allgemeine Bekämpfungslehre, der Pflanzenschutz, angeschlossen wer-
den; 2) *Angewandte Mykologie* und *Bakteriologie*; 3) *Angewandte Zoologie,* haupt-
sächlich *Entomologie.*

Von diesen bestehen nur die angewandte Mykologie und Entomologie als
Lehrfächer, wobei in der Mykologie vielfach auch allgemeine Pathologie bis zu
einem gewissen Grad in Lehrbüchern und im Unterricht behandelt wird. Je
höher dieser Unterricht steht, wie z.B. an Ihrer berühmten Hochschule, umso
mehr berücksichtigt er zugleich die allgemeine Pathologie.

Dass ich aber für die allgemeine Pathologie einen besonderen Unterricht
vorschlage, hat zwei Gründe. Erstens darf man wohl sagen, dass heutzutage für
eine allgemeine Pathologie soviel Material vorliegt, dass ihre Zusammenfassung
möglich ist, und dass dies im Interesse der Erforschung aller Pflanzenkrankheiten
gelegen ist. Zweitens sollen hier die nichtparasitären Krankheiten behandelt
werden, die bisher ganz vernachlässigt sind und die aus praktischem Bedürfnis
wie wegen ihrer theoretischen Bedeutung notwendigerweise bearbeitet werden
müssen.

Ich möchte die Gliederung eines solchen Unterrichts hier etwas näher aus-

führen.   Als Einleitung muss jeder Unterricht mit seinem Gegenstand vertraut machen und eine gewisse Menge von Anschauungsmaterial übermitteln.   Dies geschieht am besten durch eine Übersicht über die Krankheiten nach dem äusseren Krankheitsbild, wie ich sie in meiner "Einführung in die Pflanzenpathologie" gegeben habe.   Ohne besondere Berücksichtigung der Ursachen oder der inneren Vorgänge können hier einfach die Symptome beschrieben werden und es kann dabei an die allgemein bekannten Beispiele angeknüpft werden.

Als zweites Kapitel schliesst dann die allgemeine Pathologie an, in der von der pathologischen Anatomie ausgehend die morphologischen und funktionellen Veränderungen beschrieben werden.   Ihre Kenntnis erst gestattet, zu einem System der Krankheiten zu kommen, das auf cellularpathologischer Grundlage eine wissenschaftliche Einteilung gibt.

Es ist einer der wichtigsten und. zugleich zu weiterer Arbeit anregendsten Fortschritte in unserer Wissenschaft, dass H. H. Whetzel neuerdings dafür ein Einteilungsprinzip aufgestellt und damit die Möglichkeit zur Ausarbeitung einer wissenschaftlichen Klassifikation der Pflanzenkrankheiten gegeben hat.

Das Vorherrschen der ätiologischen Forschungsrichtung hat bisher die Aufstellung eines solchen Systems verhindert.   Es ist schon der Vergleich gezogen worden, dass die Medizin hierin in glücklicherer Lage war; sie hatte ihr System schon entwickelt, ehe mit der Bakteriologie auch bei ihr die Ätiologie in den Vordergrund trat.   Die Pflanzenpathologie ist aber eine junge Wissenschaft, verdankt sie doch ihren Aufschwung erst den grossen Mykologen um die Mitte des vorigen Jahrhunderts.   In ihrer Anfangszeit suchte man, wie z.B. Unger in seinem Buche "Die Exantheme der Pflanzen" (1833), die eigentlichen Krankheitsursachen in physiologischen Zuständen der Pflanze oder auch in meteorologischen Verhältnissen oder der Beschaffenheit des Standortes.   Man verwechselte also, wie wir heute sagen, Ursachen und Bedingungen; es war aber schliesslich doch eine Anschauung, der wir uns heute wieder sehr genähert haben.   Dementsprechend war denn auch Meyen (Pflanzen-Pathologie, Berlin, 1841) in seinem Lehrbuch auf dem Wege zu einer theoretischen Einteilung.   Er macht, in jener Anfangszeit der Pflanzenpathologie wohl von der damaligen Medizin beeinflusst, den Versuch, äussere und innere Krankheiten zu unterscheiden, während dann Kühn (Die Krankheiten der Kulturgewächse, 2.Aufl. Berlin, 1859) die ätiologische Einteilung in die bekannten drei Gruppen einführt, der von da an fast alle Lehrbücher folgen.   Dadurch ist die Pflanzenpathologie, die einheitlich begonnen hatte, in ihre Hilfswissenschaften zerteilt worden.

So ist auch Klebahn, der 1912 "Grundzüge der allgemeinen Phytopathologie" veröffentlichte, ganz in dieser Einteilung befangen und sagt: "Den Anforderungen einer wissenschaftlichen Darstellung genügt am besten eine Einteilung nach den Krankheitsursachen, denn nur, wenn die Ursachen bekannt sind, kann man ein richtiges Urteil über die Krankheit und ihren Verlauf gewinnen, sowie das wirklich Gleichartige aus der Mannigfaltigkeit heraus finden."

Nur Marshall Ward vermeidet (Disease in plants, 1901) diese Trennung des Gebietes und schneidet die Frage einer wissenschaftlichen Einteilung wieder an, ohne zu einer Lösung zu kommen. Jaczewski (Rep. Internat. Conf. Phytopath. and Ec. Entom., Holland 1923 [p.244]) erwähnt einen eigenen Versuch vom

Jahre 1910, in seinem Handbuch der Pflanzenkrankheiten, und spätere Versuche von Coulter 1914 und Stevens 1917. Auch Melchers hat (Phytopathology **5**: 1915 [p.297]) für die sogenannten physiologischen Krankheiten,—ein Name, der glücklicherweise allmählich aus der Literatur verschwindet—eine Einteilung gegeben. 1919 haben dann Appel und Westerdijk (Zeitschr. f. Pflanzenkrankheiten **29**: [p.176]) ein System veröffentlicht, das sich auf die pilzparasitären Krankheiten beschränkte und im wesentlichen noch die Symptome zur Grundlage hatte. Daher ergab sich bei meinem Versuch, diese Einteilung auf alle Krankheiten auszudehnen (Angew. Botanik **4**: 1922 [p.16]) nur die Übersicht der Symptome, die ich eben angeführt habe, und die wohl als Einleitung des Unterrichts brauchbar ist, aber kein wissenschaftliches System darstellt. Ich habe damals im Anschluss an Küsters Pathologische Pflanzenanatomie als cellulare Grundlagen der Krankheiten die Degeneration, die Nekrose, die Hypoplasie und die Hypertrophie erwähnt, ohne aber die Folgerung, die Aufstellung eines Systems, daraus zu ziehen. H. H. Whetzels Verdienst ist es nun, ganz neuerdings (1925) unter Aufstellung von 3 Hauptgruppen die wissenschaftliche Einteilung festgelegt zu haben. Er unterscheidet 1) regressive Veränderungen, die *Nekrosen*, die er in Plesionekrosen, degenerative Prozesse, und Holonekrosen, direktes Absterben von Zellen, Geweben und Organen teilt; 2) repressive Veränderungen, *Hypoplasen*, mit Lipoplasie (unterbleibende Differenzierung), Hypotrophie (mangelhafte Grössenausbildung) und Hypoplasie (subnormale Zellenvermehrung); 3) progressive Veränderungen, *Hyperplasen*, mit Praeplasie (vorzeitige Differenzierung), Metaplasie (Umbildung von Zellen, Geweben und Organen), Hypertrophie (übernormale Grössenausbildung) und Hyperplasie (übernormale Zellenvermehrung).

Noch einen Schritt weiter geht gleichzeitig, ebenfalls 1925, Werth, der— allerdings nur in einer kurzen Bemerkung (Angew. Botanik **7**: 1925[p.149])—nur zwei grosse Gruppen von Krankheitserscheinungen gelten lässt: die reinen Schädigungen—Nekrosen—und die Bildungsabweichungen; unter den letzteren sind, wie mir scheint mit Recht, die repressiven Veränderungen, Hypoplasien, und die progressiven, Hyperplasien zusammengefasst.

Es handelt sich jetzt nur noch darum, das System im einzelnen auszuarbeiten und insbesondere für alle wichtigen Krankheitserscheinungen die ihnen eigentlich zugrundeliegenden cellular-pathologischen Vorgänge aufzuklären.

Die Darstellung der *nichtparasitären Krankheiten* kann an die allgemeine Pathologie angeschlossen werden, wenn man sie nicht ganz selbständig machen will. Es ist kein Zweifel, dass dieses vernachlässigte Gebiet viel mehr Beachtung verdient. Denn heute hört die Bearbeitung einer Krankheit vielfach in dem Augenblick auf, wo sie als nichtparasitäre erkannt ist, wie man etwa früher damit zufrieden war, einen Parasiten entdeckt zu haben und ihn zu beschreiben. Daher fehlt es schon an der Vorbedingung der Erforschung, einer klaren Beschreibung der Symptome. So besteht die Gefahr, dass ihre Bearbeitung an die praktischen Fächer der Ackerbaulehre, Waldbaulehre usw. verloren geht, die gegenwärtig von den Sortenfragen ausgehend ebenfalls schon stark in ökologischer Richtung arbeiten. Aber für das Verständnis aller Pflanzenkrankheiten in ihren Vorgängen und ihrem Verlauf geben die nichtparasitären Krankheiten

den besten Gegenstand ab, da sie nicht durch das Hinzukommen eines Parasiten kompliziert sind. Man kann sie also sehr gut an die allgemeine Pathologie anschliessen und mit ihr als Grundlage für die Darstellung aller Krankheiten verwenden. Denn es gibt viele Fälle,—besonders klar liegen sie z.B. bei den Baumkrankheiten,—wo der Parasit erst sekundär einsetzt und eigentlich Schwächeparasit ist, wenn er auch nicht zu den fakultativen Parasiten gehört.

Überhaupt bietet sich bei den nichtparasitären Krankheiten die beste Gelegenheit, auf die Bedeutung der ökologischen Forschungsrichtung einzugehen und sie in ihren allgemeinen Zusammenhängen darzustellen, losgelöst von den Beziehungen zu den Parasiten im Einzelfalle. Die Zeit ist nicht fern, wo der Kampf gegen den Erreger bei sehr vielen Krankheiten ganz in den Hintergrund treten wird und wo man die indirekte Bekämpfung der Krankheiten in den Vordergrund stellen wird. Bei vielen Krankheiten ist das jetzt schon der Fall, wo wir auf dem Wege der Sortenwahl, Züchtung, Düngung, Änderung der Bodenreaktion vorgehen. Die Medizin hat diese Entwicklung im Kampfe gegen die Bakteriosen durchgemacht, nachdem die erste Zeit der Bakteriologie ganz dem Suchen nach äusserlichen und innerlichen Desinfektionsmitteln gegolten hatte.

Am besten zeigen diese Notwendigkeit einer selbständigen und zusammenfassenden Behandlung die vielen Erscheinungen, die teils nichtparasitäre Krankheiten, teils aber durch Parasiten verursacht sein können, wie z.B. Lithiasis an Birnen, der Milchglanz der Obstbäume, die Spitzendürre (tip burn) und das Blattrollen verschiedener Pflanzen. Dabei wird dann auch die alte Bezeichnung "physiologische Krankheiten" fallen, die man heute noch lesen kann und gegen die schon Marshall Ward 1901 sich gewandt hat (Disease in plants, p.121): Even the distinction into physiological diseases versus parasitic diseases cannot be maintained from the standpoint of the nature of the disease itself. All disease is physiological in so far as it consists in disturbance of normal physiological function, for pathology is merely abnormal physiology, no matter how it is brought about.

Aus allen diesen Gründen, ganz besonders ihrer Bedeutung als Grundlage der Kenntnis der Pflanzenkrankheiten und weil hier das Krankheitsbild nicht durch das Hinzutreten des Parasiten kompliziert ist, empfiehlt es sich, die nichtparasitären Krankheiten nicht mehr bei den parasitären zu lehren, sondern direkt an die allgemeine Pathologie anzuschliessen.

Die *Viruskrankheiten* werden dagegen, da sie sich in Bezug auf ihre Entstehung ganz wie parasitäre Krankheiten verhalten und in der Untersuchungstechnik den Bakteriosen am nächsten stehen, im Unterricht am besten als Anhang zu diesen behandelt.

Als allgemeinen Lehrgegenstand, nicht nur als Anhang zu den ätiologischen Spezialvorlesungen möchte ich auch die *Bekämpfungslehre* dargestellt sehen. Sie weist heutzutage so viele Berührungspunkte zwischen Mykologie und Entomologie auf, abgesehen von der beiden gemeinsamen Technik der Bekämpfung mit chemischen Mitteln, dass man sie am besten einheitlich darstellt. Und dann ist es doch gerade die hier im Vordergrund stehende ökologische Betrachtung, die uns zeigt, dass bei so vielen Krankheiten gar nicht der Parasit bekämpft zu werden braucht, sondern dass man durch Kulturmassnahmen die Lebensbedin-

gungen der Pflanzen bessern und dadurch dem Befall durch Krankheiten vor-
beugen oder die Parasiten ausschalten kann.

Die Bekämpfungsverfahren im Zusammenhange darzustellen ist auch aus
didaktischen Gründen notwendig. Denn der Pathologe muss den notwendigen
Überblick für die Auswahl der Verfahren gewinnen, die sich im einzelnen Falle
nicht nach irgendwelchen theoretischen Erwägungen oder der systematischen
Stellung der Parasiten richtet, sondern lediglich nach dem möglichen Erfolg. Wo
z.B. durch Sortenwahl oder entsprechende Düngung geholfen werden kann, sind
die besten direkten Bekämpfungsmittel überflüssig.

Daher darf auch die Einteilung der Massnahmen des Pflanzenschutzes nicht
irgend einem theoretischen Unterschied, wie z.B. zwischen direkter und in-
direkter Bekämpfung, prophylaktischer und therapeutischer Behandlung, folgen,
sondern sie muss sich nach dem *modus procedendi*, der Technik des Vorgehens,
richten. Von den vielen aufgestellten Einteilungen scheint mir daher diejenige
die richtige zu sein, welche mit den gegen alle Krankheiten gemeinsamen all-
gemeinen Massnahmen beginnt und dann zu den besonderen technischen Ver-
fahren fortschreitet.

Die Einteilung, der z.B. Van den Broek und Schenk (Ziekten en beschadigin-
gen der tuinbouwgewassen, Groningen, 1925) folgen, gliedert sich dann in 1)
Kulturmassnahmen im weitesten Sinne, 2) biologische Bekämpfung, 3) tech-
nische Bekämpfung, wobei der erste Teil im wesentlichen die Vorbeugung oder
Hygiene, der zweite und dritte die Therapie, d.h. die direkte und indirekte
Schädlingsbekämpfung enthalten. Bei den Kulturmassnahmen ist auch Gelegen-
heit, den staatlichen Pflanzenschutz, insbesondere die Einfuhrkontrolle, zu be-
rücksichtigen.

Mykologie und *Entomologie* sind die gegenwärtig bestehenden Teile des
Unterrichts, wenn auch der erstere in der Regel als Pflanzenpathologie bezeichnet
wird. Dies ist begründet in seiner Entstehung zu einer Zeit, da eine ausge-
bildete Entomologie schon bestand und man nun die Krankheiten mit den
Pilzen erklärt zu haben glaubte, wobei auf den Gegensatz von Krankheiten und
Beschädigungen, der nur als praktische Unterscheidung seine Berechtigung hat,
ein zu grosser Wert gelegt wurde. Vielfach hat man allerdings auch in die so
begrenzte Pathologie noch die nichtparasitären Krankheiten mit einbezogen,
aber wo dies geschah, wurden sie nur sehr kurz abgehandelt und keiner näheren
Untersuchung unterzogen. Sie blieben, als sogenannte physiologische Krank-
heiten, der immer kleiner werdende Rest, der sich nicht durch Parasiten erklären
liess. Wenn man nun die nichtparasitären Krankheiten selbständig oder in Ver-
bindung mit der allgemeinen Pathologie behandelt, so scheint mir in den Myko-
sen, ergänzt durch Bakteriosen, die ihnen in jeder Hinsicht nahe stehen, ein
genügend umfangreiches Arbeits—und Unterrichtsfeld gegeben zu sein. Auch
müssen hier, in dem botanischen Teil der parasitären Krankheiten, auch die
phanerogamen Parasiten und Halbparasiten eine Stelle finden.

Umfasst so die Mykologie gegenwärtig oft ein über ihr eigentliches Thema
hinausgehendes Gebiet, so scheint mir im zoologischen Teil die Beschränkung
auf Entomologie allein auf die Dauer nicht gerechtfertigt. Dieser Teil des Unter-
richts wird sich zwar immer im wesentlichen mit den Insekten befassen, er muss

aber die schädlichen Wirbeltiere und niederen Tiere mit umfassen, die im Unterricht jetzt entweder ausfallen, oder, wie es merkwürdigerweise in einigen Ländern mit den Nematoden der Fall ist, in einem anderen Unterricht behandelt werden.

Für diese beiden Fächer gibt es schon zahlreiche und gute Lehrbücher, da sie ja die bisher herrschenden Arbeitsrichtungen vertreten. Denn die heutige Pflanzenpathologie hat sich tatsächlich aus der mykologischen Forschung entwickelt, während die entomologische schon lange selbständig besteht und es insbesondere als Forstentomologie zu hoher Blüte gebracht hat. Doch ist in den verschiedenen Ländern in sehr ungleicher Weise für den Unterricht gesorgt, der, wo er besteht, meist den praktischen Pflanzenschutz im Auge hat, während viele Länder in der Ausbildung von Pflanzenpathologen noch zurückstehen. Über das Fehlen einer eigentlichen Berufsausbildung in Deutschland hat sich Appel 1919 (Angew. Botanik 1: 1919 [p.10]) ausgesprochen und seitdem ist darin keine wesentliche Änderung eingetreten. Auch der internationale Zoologenkongress in Zürich 1925 hat sich sehr energisch für bessere Ausgestaltung des entomologischen Unterrichtes eingesetzt. Ich möchte hier auf die sehr zweckmässig eingerichteten Lehrgänge besonders hinweisen, die ich in dem landwirtschaftlichen Forschungsinstitut in Pusa, Indien, kennen gelernt habe, wo ein genaues Programm für einen einjährigen Ausbildungskursus in Entomologie und für einen zweijährigen Kursus in Mykologie aufgestellt ist.

Ein offener Punkt in dem vorgeführten Programm ist noch die bisher nicht erwähnte Kenntnis der praktischen Landwirtschaft, bezw. der so verschiedenartigen Anbaumethoden der einzelnen Kulturpflanzen. Auch hierin zeigt sich die Vielseitigkeit der Ansprüche, welche die Pflanzenpathologie an den Forscher stellt. Es müsste also dem Studierenden ausser der Anschauung auf Exkursionen und dem Versuchsfeld Gelegenheit gegeben werden, wenigstens eine Vorlesung über Pflanzenbau zu hören. Es darf daran erinnert werden, dass der verstorbene H. Maxwell Lefroy diese Kenntnis derjenigen der ganzen Schädlingskunde an Bedeutung gleichgeschätzt hat, wenn er sagt (Notes on the work of entomological assistants, Calcutta): It must be borne in mind that a knowledge of agriculture is as important as a knowledge of the pest; a preventive or a remedy, to be practicable, must fit in with established local practise.

Und L. Hiltner, den wir in der praktischen Nutzanwendung wissenschaftlicher Forschungen sehr wohl einem Manne wie J. Kühn an die Seite stellen dürfen, hat dieses ökologische Programm und seine Bedeutung für den Pflanzenschutz so formuliert: "Der Untersuchung des Saatgutes und der Berücksichtigung der Ernährungsansprüche der einzelnen Arten und Sorten der Kulturpflanzen, der Prüfung der Einwirkung physikalischer und chemischer Bodeneigenschaften und somit auch des Einflusses der Düngung und der Bodenorganismen, der gebührenden Berücksichtigung der Phänologie, sowie der Klima- und Witterungskunde ist im Rahmen des gesammten Pflanzenschutzes die gleiche Bedeutung zuzumessen, wie etwa der Entomologie und der Pilzkunde. Nicht immer gelangt der Spezialforscher auf allen diesen Gebieten zur wahren Tiefe der Erkenntnis, sondern häufiger wird dies jenem Forscher beschieden sein, der sich bestrebt, dem Zusammenhang der Dinge nachzugehen."

Das ist es auch, was die praktische Landwirtschaft, der Pflanzenbau, vom Pflanzenschutz verlangt. Die Wirtschaftsführung und Kulturgestaltung sollen so eingerichtet werden, dass die Übertragung der Krankheiten und die Vermehrung der Erreger durch Sortenwahl, Fruchtfolge, Bodenbearbeitung, Düngung und andere Massnahmen des Pflanzenbaues so weit als möglich verhütet werden, ohne dass besondere und kostspielige Bekämpfungsverfahren notwendig sind.

Somit laufen beide Tendenzen, die vertiefte wissenschaftliche Behandlung der Krankheiten und die praktischen Anforderungen des Pflanzenschutzes, auf dasselbe Ziel hinaus, auf die ökologische Forschungsrichtung. In jeder Wissenschaft wechseln die herrschenden Forschungsrichtungen im Laufe der Zeit, womit nicht gesagt ist, dass dabei die bisher erfolgreich beschrittenen Wege ganz verlassen werden. Wie in der allgemeinen Botanik heute die Systematik und Anatomie von der Physiologie abgelöst worden sind, ohne jene beiden dadurch überflüssig zu machen, so sind auch in der Pflanzenpathologie z. B. in der Erforschung der Krankheitserreger oder der Verwendung chemischer Mittel neben den neueren Arbeitsweisen immer noch wichtige Fragen zu lösen.

Aber man hat bisher oft allzu einseitig nur die Parasiten beachtet, während die Ökologie die kranke Pflanze wieder in den Vordergrund stellt. Sie muss von unserer Seite umso mehr bearbeitet werden, als sie auch im Pflanzenbau selbst heute schon eine wichtige Rolle spielt. Im Ackerbau, im Obstbau und in der Forstwirtschaft wählt man heute Arten und Sorten nicht mehr blos nach ihren reinen Leistungen aus, sondern man berücksichtigt mehr und mehr ihre Ansprüche an den Standort und ihre Abhängigkeit von demselben. Je grössere geographische und besonders klimatische Unterschiede ein Land aufweist, umso erfolgreicher wird die pflanzengeographische Charakterisierung der Sorten sein. Diese Richtung steht in so enger Beziehung zum Pflanzenschutz, dass er selbst ein Arbeitsgebiet verlieren würde, wenn er sich dieser Fragen nicht annähme. Auf den Pflanzenschutz übertragen, ist die ökologische Richtung nichts anderes als die alte Prädispositionslehre, die Sorauer vor vierzig Jahren aufgestellt und immer wieder vertreten hat. Sie nimmt zugleich mit einer besseren Naturerkenntnis die Bestrebungen der früheren Pflanzenpathologen vor 100 Jahren wieder auf, die noch keine Krankheitserreger im heutigen Sinne kannten, dafür aber umso deutlicher die Abhängigkeit der Krankheiten von Faktoren der Umwelt fühlten. Auch die Medizin arbeitet in gleichem Sinne und hat diese uns bekannte Prädispositionslehre gewissermassen übernommen, wenn sie in der *Konstitutionspathologie* die für gewisse Krankheiten anfälligen Typen festzustellen versucht.

Die ökologische Forschung, die so viele Einzelfragen zusammenschliesst, setzt aber umfassende Kenntnisse der Pflanzenkrankheiten voraus. Sie wird daher am besten auf der Grundlage einer allgemeinen Pathologie betrieben. Wenn wir den Unterricht heben und im Sinne dieser allgemeinen Pathologie ausbauen, so wird damit auch die Forschung wirksamer gestaltet, deren der Pflanzenschutz zur Erfüllung seiner praktischen Aufgabe bedarf. Die Einsicht ist heute allgemein, dass in allen Fragen der landwirtschaftlichen Urproduktion die Zeit der empirischen Fortschritte vorbei ist und dass nur gründliche wissenschaftliche Arbeit uns weiter vorwärts bringt.

THE TERMINOLOGY OF PHYTOPATHOLOGY[1]

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The rise of new concepts and the modification of old ones by accretion or restriction are the inevitable accompaniments of the growth and development of any science. They inhere in the very nature of such growth and are the products of the process. Scientific terms are but names for these concepts and terminology the science of their correct application and use.

Few of the biologic sciences have had so rapid and astonishing a development as plant pathology. Its intrinsic interest and its economic importance have combined to place it, in the short space of less than half a century, in the forefront of applied sciences in agriculture. Today it ranks well along with bacteriology and medicine in its importance to the welfare and progress of mankind. Its growth during the last two decades, at least in America, has been phenomenal. Its votaries crowd the temples of graduate learning and their tracts fill the pages of journals, bulletins, and books. The rapidly mounting mass of new facts and experimental data has called forth new concepts and radically modified old ones, but our terminology has not kept pace with this growth. Old terms have been called upon to do double, triple, or even quadruple duty, with a consequent confusion often sadly involved. Terms have been plucked from sister sciences to serve in a new and strange environment, usually with little thought as to their applicability. Worse still is the inexcusable use of a pathological term clearly defined and limited in its application to designate another pathological concept not only quite different in kind but already provided with a well recognized and distinct name of its own.

The coinage of terms to clothe the new-born concepts of our science has been singularly rare. This will be regarded with satisfaction and approval by the indolent and conservative amongst us, but it has resulted in a confusion and circumlocution of expression comparable to the situation in a prolific family where the sons of succeeding generations are blessed with the same Christian name. New terms for new things and new ideas are indispensable requisites for clear thinking and accurate expression.

The terminologic situation in plant pathology today is in large part the result of its historical development. Prior to the middle of the nineteenth century plant pathology had a development more or less independent of other plant sciences. It had a well organized and generally accepted terminology corresponding to a considerable degree with that of human pathology. Then came the

revolutionary discoveries of DeBary and other workers on the parasitic relationship of the fungi associated with diseases in plants. Emphasis was abruptly shifted from the diseased plant to the causal organism. Mycology took the stage and promptly absorbed the major interest and attention of most of the early workers whom we are all too prone to regard as plant pathologists. DeBary and his followers were mycologists and only very incidentally interested in the pathologic effects of the fungi which they studied. Even the pathologists among them, of whom Julius Kühn is to be regarded as leader in the modern field, were dominated by the etiologic or economic aspects of the subjects. For fifty years the pathogeneticists controlled the destinies of our science. To a few predispositionists led by Sorauer was left the task of bearing the torch of pathological morphology and physiology all but extinguished by the downfall of the auto-geneticists whose great exponent was Franz Unger.

The rise of bacterio-phytopathology in America during the latter quarter of the 19th century due to the epoch making discoveries of Erwin F. Smith and his co-workers but served to emphasize the etiologic aspects of our science. To Ernst Küster more than to any other man belongs the credit of reviving and organizing our knowledge of phytopathological anatomy during the modern era. But so overwhelming has been the interest in the etiologic aspects that his work has far too little recognition and influence even at the present time. The economic phase of plant pathology so sharply brought to the fore by the discoveries of Prevost, Kühn, and Jensen on seed disinfection and by Millardet on protection by spraying have been more potent in correcting the etiologic over-balance, but have also contributed to the terminologic confusion.

Even a casual survey of the literature of plant pathology will at once discover the dominating influence of mycologic terminology, and a confusion of usage largely attributable to our inclination to borrow and adapt rather than invent and build.

So long as phytopathology remained a science for investigation and application alone this disordered state of its terminology, while deplorable, was still tolerable. It matters little perhaps to investigators whether or not they understand each other clearly. Investigation is commonly assumed to be a private matter and obscurity of expression feeds the flame of controversy so dear to most of us.

The layman accustomed to a restricted vocabulary and said to require his intellectual pabulum in the vernacular has been commonly made the excuse for absurd and inaccurate use of terms. Poverty of technical expression and misuse of terms in teaching has likewise been laid at the door of our students, who are strangely supposed to be incapable of learning and of using new terms. This is a charge wholly denied by the alacrity and acumen with which they adopt the current slang phrases of the day.

Twenty years of association with farmers and students in the study of plant diseases and their control completely absolves them both, in my opinion, of incompetency and disinclination to think and speak with accuracy and precision. Whatever of validity there may be in the excuses of investigators for

careless and illogical use of terms in expressing their ideas, it does not hold in the case of teaching. Logical organization and precision of expression are the very essence of good teaching whether in class room or field. Even in the realm of research orderly thinking and clear expression must sooner or later prevail if our science is to attain to that position of authority, confidence, and dignity which it deserves.

The teaching of plant pathology is a very recent development. The first university chairs in this subject were established in colleges and universities less than three decades ago. Even now they are but few. Many of the courses today masquerading under the name of plant pathology are but mycology or a bastard progeny, resulting from an illegitimate cross between mycology and the art of plant disease control. The false pedagogy of, "many facts and few principles" so prevalent in college courses has resulted in a shallowness of treatment and dearth of understanding that is only too often reflected in the amateurish contributions which flood our technical journals and institutional publications. This has in no small degree contributed to the confusion and quagmire of terminology in which we flounder or supinely sink.

My experience of twenty years in an attempt to organize the subject matter of phytopathology for purposes of university teaching has perhaps over-emphasized the importance of terminological order and clarity. An attempt to formulate, define, and designate current concepts in this field for text book purposes has convinced me that no more necessary and important problem confronts the pathologists of this generation than that of an effort to put our terminology in order.

The prevailing point of view in plant pathology for 75 years has been and still largely remains almost exclusively etiological, with mycology and bacteriology dominating our thought as well as our terminology. Not forgetting (as doubtless we shall not be allowed to) the debts we owe to sister sciences and their devotees, it is time that our science assert its individuality not only in name but also in its thought and language.

It is not my purpose in this paper to present a full discussion of the subject. The main features of such a reorganization and definition I shall leave for my forthcoming text on the Elements of Plant Pathology. I shall attempt today only to bring to your attention a few of the outstanding incongruities and absurdities in our present terminological practice.

I have already referred to the dominating influence which mycology has exercised on phytopathological terminology since the middle of the nineteenth century. Only in the last decade have we begun to emerge from this domination in spite of cogent protests voiced from time to time by prophets crying in the wilderness. No more striking evidence of its baneful influence can be asked than the prevalent practice of treating the pathogene and the disease as synonymous concepts. I refrain from embarrassing you by quotations from your own publications. Few of us are innocent of this grossest of errors.

While no one can gainsay the importance of the etiologic aspects of disease in plants, no legitimate warrant can be found for its glorification to the dis-

regard of other equally important features of the subject. Worse still is the prevalent tendency to drag in and house under the phytopathological roof matters only remotely related to the problems of disease. We may cite, for example, the practice of introducing into a treatise on a plant disease the endless details of the cultural reactions of the pathogene on miscellaneous artificial media. While occasionally interesting and sometimes possibly useful from a physiological view point, their phytopathological significance is usually nil.

Plant pathology is the science of abnormal plant physiology. That is, of course, abnormal physiology of the suscept, not of the pathogene, as one might be led to think from a casual perusal of the literature of our subject. Disease, as Morstatt has recently emphasized, is a physiological process, or better, perhaps, an interrelated group of processes. It is not a condition, as almost universally stated. The conditions we have in mind are the expression of the disease processes. They are the symptoms of disease.

It is self evident that any accurate and logical use of phytopathological terms will be motivated by an accurate and clearly defined concept of disease *per se*. However we may clothe the concept in making a definition of disease, its essential processional character must be emphasized. The disease concept must condition and rationalize all other concepts of our science and consequently its terminology.

There must be no evasion of the fact that the diseased plant is the central figure in the phytopathological drama. The causal organism, where such is involved, must be relegated to its distinctly secondary rôle. Parasitism may be a series of physiological interactions *between* the parasite and its host. Disease is the composite of reactions of the plant to the causal factor or factors operating upon it. The effects of the plant upon the etiologic agent is not an essential feature of disease.

In order that you may have before you my present conception of a logical organization and presentation of the subject matter of plant pathology, I present the outline for such an arrangement of the data on an individual disease. This plan of treatment I have long used, with slight modifications from time to time, in presenting the subject to my students. It is with a pleasure, akin, perhaps to the effects of flattery that I occasionally encounter in the writings of my contemporaries evidence that this arrangement has somewhat at least of logic to recommend it.

OUTLINE FOR ARRANGING DATA ON A GIVEN DISEASE
(NAME OF THE DISEASE)

SUSCEPTS
PLANTS AFFECTED
VARIETAL SUSCEPTIBILITY

DISEASE
NAMES
HISTORY AND RANGE

IMPORTANCE
SYMPTOMATOLOGY

Morphologic Symptoms. . . . . ·
Signs. . . . . ·
Histologic Symptoms. . . . . ·

ETIOLOGY

Name, history and classification of the pathogene. . . . . ·
Pathogenicity. . . . . ·
Life history. . . . . ·
    The Primary Cycle. . . . . ·
        Pathogenesis. . . . . ·
            Inoculation stage. . . . . ·
            Incubation stage. . . . . ·
            Infection stage. . . . . ~. . . . . ·
        Saprogenesis. . . . . ·
    The Secondary Cycles. . . . . ·
        Pathogenesis. . . . . ·
            Inoculation stage. . . . . ·
            Incubation stage. . . . . ·
            Infection stage. . . . . ·
        Saprogenesis. . . . . ·

EPIPHYTOLOGY

CONTROL
EXCLUSION
ERADICATION
PROTECTION
IMMUNIZATION

BIBLIOGRAPHY

    This outline will serve as a guide to the terminological ramble on which we are about to embark. Many of the terms upon which I shall dwell appear here in what I conceive to be their sequential relation to each other.

    Let us consider for a moment the disease relationship involving a causal organism. The discovery of the parasitism of certain fungi in other plants promptly led to the adoption of the couplet "parasite and host" to connote that relationship. This connotation was originally used to indicate the food relation which is alone the essential feature of parasitism. While it has always been recognized more or less clearly that the causal relation of such organisms to disease is essentially different from their parasitic relation, the use of the same terms to connote both has led to a confusion of the two concepts. The introduction of the term pathogene and its general adoption by plant pathologists has been a logical step in the right direction but failure to provide a term to designate the other part to the pathologic relationship has resulted in the absurd usage of "pathogene and host." To meet this situation I have coined and now use the term *suscept* to designate the plant. Thus we have the couplet, "pathogene and suscept" to connote the pathologic relation. We have freed the

combination, parasite and host of a false implication and leave no excuse for the incompatible connotation, "pathogene and host."

Turning now to the subject of the classification of diseases we find a situation not only illogical and indefensible but decidedly perversive of rational terminology. The all but universal basis used for grouping plant diseases is the taxonomic classification of the causal organisms. And this is called classifying plant diseases! Here again the unfortunate influence of etiologic domination is clearly apparent. Since disease is a physiologic process and specific diseases, interrelated groups of such processes, it requires no special perspicacity to discern the absurdity of such a basis for their classification. There might be some excuse for such an arrangement were there any consistent correlation between kinds of pathogenes involved and the character of the diseases they produce. No such correlation is discoverable. This basis for classification has led to such groups names as "physiologic diseases," as though all diseases were not physiologic. If such a group of diseases is to be set apart under a separate designation the term physiogenic will more accurately express the concept.

The only logical basis for classifying diseases in plants is the nature of the disease processes themselves. On this basis all diseases of plants fall into three groups: (1) That in which the predominating processes lead directly to the degeneration and death of the cells, *necrosis*; (2) that in which they result in a slowing up or halting a normal development of the protoplasts, *hypoplasis* and (3) that in which they are expressed in over development of some sort, *hyperplasis*. This manner of grouping brings together those diseases which have pathologic characters in common. It provides a rational and natural organization of the vast and growing number of plant maladies known to science and requires no troublesome and unrelated addenda groups such as bedraggle the systems now in vogue. And most important of all it directs attention to the fundamental and essential character of plant pathology, the study of *disease* in plants.

This discussion of nature and classification of diseases leads us next to a consideration of some of the terms employed in symptomatology which deals with the evidences of disease. These evidences are of two sorts. symptoms and signs; the former being expressions by the plant itself of the disease process, the latter other evidences, such as pathogene structures, emanations, and the like. These two classes of symptomatological evidence are clearly distinct, yet the terms designating them are constantly misapplied in phytopathological discussions and writings. Symptoms which are the conditions resulting from pathogenic processes are constantly confused with the disease itself as most definitions of the latter give witness. The term "symptom complex" is a more accurate designation of the concept which we commonly visualize under the name symptom. The classification of symptoms naturally follows that of diseases giving us three main classes, the *necrotic*, the *hypoplastic* and the *hyperplastic* types. The names of symptoms and symptom complexes have arisen like the names of diseases, with no regard to an orderly or logical system, and we must perhaps accept the motley array in both cases with such grace as we may. It does not follow, however, that we should continue to apply these names in the

shiftless and confusing manner which now characterizes our usage. Each term should designate a specific and well defined concept. The term chlorosis will serve to illustrate the confusion now prevalent in symptomalogical terminology. Chlorosis has been so variously used since its early introduction into phytopathological writings that one seeks in vain for authority as to its logical and proper application. Its almost universal employment to designate the dominating symptom of most mosaic diseases of plants appears to offer the best guide to its proper application and usage. Our present knowledge of the chlorophyllous disturbances incident to these maladies suggests at once that they are primarily hypoplastic in character. They are the expressions of inhibitions or haltings in the development of chloroplast growth or chlorophyll production. There are, on the other hand, many cases among diseases of plants in which degeneration and destruction of chloroplast structure together with concomitant breaking down of the chlorophyll itself are the immediate results of the primary pathogenic processes involved, that is, they are necrotic in character. It is at once evident then that to apply the term chlorosis to both these expressions of disease is to invest it with a double and confusing significance. Yet this is constantly done. This practice cannot be excused on the grounds of lack of satisfactory and acceptable terms. Yellowing or icterus has long been used to designate the chromatic expression of chlorophyllous degeneration. We shall therefore clear away much of the current confusion in our thinking and discussion if we rigorously restrict the term chlorosis to that achromatismic symptom resulting from hypoplastic processes in chloroplast and chlorophyll development and apply the term yellowing or icterus to that plesionecrotic symptom expressive of the color changes resulting from degeneration processes in these cell organs and products. Nor should the fact that such degeneration frequently occurs in the advanced stages of certain mosaic diseases entice us into a misconception of the fundamental nature of the pathologic processes involved and the character of their predominant symptomatic expression.

A similar situation exists with respect to a number of the other numerous symptomatological concepts and terms. In my forth-coming text book I have endeavored to define these concepts and designate the terms most applicable in each case as well as to arrange them under a classification compatible with the types of the processes which they express.

Investigation in the etiologic field has undoubtedly dominated up to the present, and the contributions bulk largest and out of all proportion to their significance in relation to other phases of plant pathology. Here one might naturally expect to find more of order, accuracy, and consistency in the application and use of terms. An examination of the situation, however, discloses a confusion and ambiguity of practice no less deplorable than in other directions.

The situation may be illustrated by the consideration of a few of the more flagrant cases. I have already referred to the inexcusable synonymizing of the disease and the pathogene concepts in the matter of their names. But it does not end there. Historical discussions dealing with the pathogene constantly involve a confused interweaving of historical facts and deductions respecting

the disease, many of which have no relation to or bearing upon the history of the pathogene as such. The reverse quite as frequently occurs. While the intimate relations of the two in their historical aspects are at some points natural and undeniable, this cannot be offered as a legitimate reason for loose thinking and discussion in treating them. Numerous cases will occur to most of you in which many of the facts respecting the disease and its pathogene have had a long and distinct historical development, prior to the discovery of their etiologic relationship. The important point is that whether treated separately or together the conceptual identity of each is to be clearly maintained.

Pathogenicity is the ability of an organism to produce disease. It can, of course, be exercised only under conditions requisite to its expression. It is not to be confused with virulence which is the measure of pathogenicity. The term pathogenesis has been used to denominate this concept but current usage undoubtedly favors pathogenicity. Moreover, pathogenesis expresses more fittingly another concept which I shall present shortly. Variation in pathogenicity among strains or races of a pathogenic species is variously designated; biologic specialization and physiologic specialization being the more commonly used terms. We shall more accurately express the concept if we use the expression pathologenic specialization and speak of pathologenic races or strains instead of biologic or physiologic races, both of which are more inclusive terms.

Perhaps nowhere in plant pathology is terminological usage more inconsistent and perplexing than in our discussions of the life history of the causal organism. Here again the influence of the mycological point of view and our attempt to adapt its terms to phytopathological concepts largely explain the tangle in which we find ourselves.

Since a pathogene is any organism capable of inducing disease, it naturally follows that in applying the term "life history" we must keep in mind primarily pathogenic activities. The life history of a pathogene then is the story of its activities as a disease producer in all the different forms and relationships through which it may pass. Our division of the life history into cycles, phases periods, etc. will therefore be somewhat different in both content and sequence from those into which the mycologist, the bacteriologist, the entomologist, or any other biologist with his peculiar point of view will conceive and order life history concepts respecting the same organism. This does not argue that our conceptual content expressed by these terms is fallaceous or that our sequential arrangement of the life history phenomena are incorrect any more than his use of these terms indicates that he is in error. It is perhaps unfortunate and confusing that we should use a term which we find at hand in a different sense from that in which others legitimately employ it. This is, however, but one of those difficulties in lingual practice for which we are no more responsible than the rest of mankind. It is our responsibility, however, that we apply these terms consistenty with our point of view.

The life history of a pathogene consists of distinct units of continuous existence, initiated by the transfer of some portion of the organism to a new environment and ending with its activity therein. Such units of existence we

may properly designate as life cycles. For example, a life cycle of a pathogenic fungus is initiated by the transfer of a spore to an infection court and is completed on the death of the last bit of mycelium in the lesion produced.

Life cycles are either primary or secondary. Those which are initiated first after a period of rest or inactivity on the part of pathogene and suscept are to be designated primary cycles; in temperate regions, those originating in the spring or summer from overwintered pathogene structures; in tropical countries, those originating just after the dry season. Secondary cycles are those originating during the growing season. Both expressions are now established in our terminology but our usage of them is often neither logical nor consistent.

A pathogene usually exhibits during any life cycle two rather distinct phases. That phase of the cycle during which it becomes and remains associated primarily with the living tissues of the suscept I designate as pathogenesis. This is the phase during which it exercises its pathogenicity. Following pathogenesis, sometimes in part coincidental with it, many pathogenes continue their existence without pathogenic activity. This I designate for want of a better term, saprogenesis. Saprogenesis is not infrequently wanting in some or all the life cycles of certain pathogenes.

The time at my disposal will not permit a further exposition of these concepts nor a defense of the terms I have chosen to employ for their identification. I am well aware that cases may be cited in which satisfactory application of these terms cannot be made. They are exceptions which are neither numerous nor vital.

As pathologists our major interest in the pathogene is with its activities during pathogenesis. This phase falls rather naturally into three stages for which we find ready at hand and long in use the terms, inoculation, incubation and infection. I prefer for cogent reasons to speak of these as stages rather than periods, as is more commonly done.

The inoculation stage begins at the moment when the inoculum leaves the source of inoculum and ends with its deposition in the infection court. Or, to put it another way, the inoculation stage comprises all the phenomena involved in the transfer of the inoculum from the source of inoculum to the infection court. Inoculation is the act of transferring the inoculum to an infection court. Its use to designate the transfer of spores, mycelium, bacteria, etc. to culture media, or soil, and the like, is inconsistent with its conceptual content as a phytopathological term and should be discontinued. One cannot inoculate that which cannot exhibit disease. Disease is an attribute of living things only.

The incubation stage begins at the moment when the inoculum is deposited in the infection court and ends at the first reaction of the suscept to the activities of the pathogene. Germination, growth, and development of the inoculum, occurring between these limits, even ingress of the pathogene into the suscept are phenomena of the incubation stage. Incubation is frequently used to refer in various ways to the disease rather than to the pathogene, as for example the much used term, "incubation period." Current usage of this expression is variable, loose, and inconsistent. It is frequently employed to cover roughly

the time elapsing between inoculation and the first observed evidences of disease. The ambiguity and inappropriateness of such a usage will be evident upon reflection. Disease, as we have defined it, can scarely be thought of as incubating. Incubational phenomena are characteristic of living things only. Disease is a process, not a concrete thing. The time elapsing between inoculation and the first observed symptoms is better designated by the expression "latent period" of the disease. This will however, commonly include the incubation stage as I have defined it, together with the early stages of infection. Accuracy of expression and clarity of thinking will be better served if we entirely abandon such usage and employ the phrase "latent period of infection" to designate the time elapsing between the end of the incubation stage of the pathogene and the first visible evidences of infection in the suscept.

The infection stage is that portion of pathogenesis during which the suscept is exhibiting reactions to the activities of the pathogene. It covers the period during which the pathogene is exhibiting its pathogenicity and the suscept its susceptibility; the diseased conditions develop, the symptoms appear. The infection stage begins with the first response of the plant to the activities of the causal organism in a given lesion and ends with its final reaction thereto. Here again we find the greatest diversity of usage and confusion in the application of the word, infection. To speak in a manner implying that man or any other agent of inoculation can or does infect a plant is manifestly absurd. Man, insects, the wind, or any other agent may inoculate a plant but the pathogene alone can infect it. Equally indefensible is our common use of the word in such expressions as "to infect the soil," "infected soil," "soil infection," "source of infection" and the like. The term infection is not infrequently employed to designate ingress, that is, entrance or penetration of the pathogene through the external covering of the suscept to the tissues beneath. Ingress is fundamentally a phenomenon of incubation since it is essentially an independent activity of the pathogene, and is often completed with no evident response on the part of the suscept. The fact that not infrequently infection phenomena may result from the activities of the pathogene at some stage of ingression does not validate the confusion of the two concepts or justify the synonymous use of the terms designating the two processes.

Again, infection is frequently used in a manner to imply its restriction to the initial response of the suscept to the attack of the pathogene. Infection is a continuous procession of responses as protoplast after protoplast in the cellular complex reacts to the invading organism. It ceases only with the registration of the last response of the living substance in the involved suscept structures. Here again a clear distinction is to be made between invasion of the tissues by the pathogene and the accompanying or resulting infection. Infection responses may occur at some distance beyond the zone of invasion, as in the case of many wilt diseases, or these responses may be quite undetectable, probably in some cases wanting, within a part of the invasion zone. That invasion of the tissues of a plant by another organism may occur without resultant infection seems evident in well authenticated cases, such as that of the parasitic *Lolium* fungus

and of *Eocronartium* in mosses. Parasitism and disease are not co-respondent processes. Either may occur without the accompaniment of the other. Their common concomitant occurrence even, cannot be taken to argue causal connection, as is generally implied in phytopathological discussions.

Employing the term infection synonymously with lesion is less confusing; it is however, unnecessary, but I fear this usage is too firmly established in our terminology to yield at present to argument.

Perhaps most confusing of all is the combination "infection period." One has but to scan a month's output of phytopathological literature to discover the personal idiosyncrasies of usage to which this expression is subjected. Many authors employ it to nominate periods of time during which conditions, especially weather conditions, are favorable to inoculation, incubation, and initial or latent infection, a usage more or less synonymous with the "incubation period" of other authors. Whatever its application, it is seldom clear whether the author refers to the pathogene or the disease, or lumps them together in nebulous confusion. A distinct gain in accuracy of thought and expression would be attained by the general avoidance of the word "period" in couple with the terms inoculation, incubation and infection. Since disease processes are concomitant only with infection we shall avoid most of our current inconsistencies in the terminology of the life cycles of pathogenes by the use of the couplets, inoculation stage, incubation stage, and infection stage, respectively.

The facts and deductions having to do with the influence of environmental factors on the occurrence, destructiveness, and other peculiarities of diseases constitute a unit aspect of our science designated by such terms as, "environmental factors," "ecology," and "epidemiology." Pertinent objections can be raised not only to each of these in particular but more cogently to the lack of uniformity and consistency in the naming of this phase of the subject. We have long had at hand the etymologically consistent term epiphytotic to designate the destructive occurrence of a disease. We shall avoid the inconsistent implication of epidemiology and the embarrassments of the already preempted "ecology" by the rational coinage and use of epiphytology in this connection.

We come finally to the subject of plant disease control. By the expression "control of plant diseases" is meant a profitable reduction in the injury they may cause. In no other phase of our science has there been so little effort to organize the vast accumulation of data derived from observation, experimentation, and practice into a coherent and ordered whole. The daily grist is dumped promiscuously, burying and bewildering the struggling novitiate in his efforts to comprehend and use it. Here we find unorganization and terminological confusion at their worst.

For many years now I have offered a course at Cornell University on the "Principles of plant disease control" in which I have sought to give the student a comprehensive and organized view of our knowledge of the subject. I find that all methods as yet proposed for the control of plant diseases are based upon one of what I choose to call the four fundamental principles, exclusion, eradication, protection, and immunization. I am well aware that in adopting these

terms I appear to violate the very thing for which I plead in this discourse. That these terms have a great variety of application in lay speech and writing as well as in scientific communication cannot be denied. That fact is indeed to be emphasized here. Nevertheless, even the boldest must hesitate at times to load a conservative and sluggish constituency with a strange coinage, however appropriate and shining it may appear to the writer himself. If it be conceded, however, that in the language of phytopathology these terms shall have only a technical significance, clearly defined and understood, they will be found to serve the purpose admirably.

By exclusion is meant preventing to a profitable degree the entrance and establishment of a pathogen in an uninfested area, as in a garden, field, region, state, or country. By eradication is meant the more or less complete elimination or destruction of a pathogen after it is established in a given area. By protection is meant the interposition of some effective barrier between the susceptible parts of the plant and the inoculum of the pathogen. By immunization is meant the development by natural or artificial means of an immune or highly resistant plant population in the area infested with the pathogen to be combatted.

It will be observed that the measures employed in applying the first two principles are directed primarily toward the pathogen, those of protection and immunization toward the suscept.

This brief outline of the organization of the subject matter of control and its carefully considered terminology, if generally adopted, would, I am convinced, greatly conduce to more rational and more productive efforts in our investigations and practices in plant disease control.

I may be again permitted to stress the fact that many of us masquerading as plant pathologists are, from training and inclination, mycologists, bacteriologists, or what not in our point of view. To such naturally my appeal for specificity and consistency in phytopathological terminology will have little appeal and less response. But to that rapidly growing host of young workers whose eyes seek the true path of phytopathological progress, I commend it for thoughtful and unbiased consideration.

FORSCHUNGS- UND LEHRTÄTIGKEIT AUF DEM GEBIETE DER PFLANZENPATHOLOGIE IN DEUTSCHLAND[1]

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Die Pflanze ist ein Lebewesen, genau so wie der Mensch und das Tier. Sie wird geboren als ein kleines, zartes Gebilde, welches nur ganz allmählich lernt, sich selbst zu ernähren, sie nimmt im Laufe ihrer Lebenszeit zu an Umfang, sie besitzt die Kraft der Empfindung, indem sie auf den Reiz des Lichtes, der Wärme, der Verwundung reagiert, sie ist mit allen ihr zu Gebote stehenden Mitteln auf die Erhaltung der Art bedacht, sie stirbt schliesslich und fällt der Verwesung anheim ganz wie wir Menschen. Es bedarf hiernach keines besonderen Beweises mehr, dass sie auch erkranken kann und dass sie im erkrankten Zustande weniger leistet als im gesunden.

Menschheit und Tierwelt bedürfen der Pflanze unbedingt, denn sie allein verfügt über das Geheimnis, wie aus Steinen Brot, d.h. aus unorganischer Bodenmasse die für die Erhaltung von Mensch und Tier unerlässlichen organischen Nährstoffe hergestellt werden. Alle Versuche, der Pflanze ihr sorgsam gehütetes Geheimnis zu entreissen, sind bisher missglückt.

Aus diesen beiden Hinweisen ergibt sich die Notwendigkeit der Pflanzenpathologie. Kranke Pflanzen hat es jedenfalls gegeben ebensolange als es Pflanzen überhaupt gibt. Beachtung durch den Menschen haben sie wohl aber erst nach der Sesshaftwerdung der einzelnen Völker und der damit verbundenen Bodenständigkeit des Ackerbaues gefunden.

Die ersten menschlichen Bemühungen pflanzenpathologischer Natur haben sich in rein praktischen Bahnen bewegt. Sie hatten zum Endziel lediglich die Beseitigung des Krankheits- oder Schadenerregers. Entsprechend der in der Vorzeit herrschenden Unkenntnis auf naturwissenschaftlichem Gebiete waren auch die zur Anwendung gebrachten Mittel beschaffen. Bis weit über das Mittelalter hinaus bestanden sie in der Verrichtung kirchlicher Gebete, im Läuten der Klosterglocken, bei Heuschreckenplagen in dem einfachen Einsammeln mit der Hand, in der Benetzung der Samen mit Oel, Urin und ähnlichen Flüssigkeiten, in dem Vergraben einer Kröte u.A.m. Bis in das 19. Jahrhundert hinein blieben diese mangelhaften Zustände bestehen. Die christliche Kirche war der Erforschung natürlicher Vorgänge nach Ursache und Wirkung nicht günstig gesinnt. Auch fehlte es bis in die Neuzeit hinein an den nötigen Hilfsmitteln. In vielen Fällen fehlen solche heute noch. Mit dem Beginn des 18. Jahrhunderts machen sich in Europa die ersten Ansätze zur Begründung einer Pflanzenpathologie auf wissenschaftlicher Grundlage bemerkbar. Soweit

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Deutschland hierbei in Frage kommt, sind zwei Tatsachen bemerkenswert. Einmal der Umstand, dass der Fusspunkt der pflanzenpathologischen Wissenschaft in der Aufstellung von Systemen zu einer noch gar nicht vorhandenen Wissenschaft bestanden hat und weiter der Umstand, dass das erste deutsche wie überhaupt das erste Lehrbuch der Pflanzenpathologie, welches im Jahre 1794 erschienen ist, einen Arzt zum Verfasser hat.

Systeme der Pflanzenkrankheiten haben geliefert: Zwinger, 1708; Eysfarth, 1723; Zallinger, 1779; Batsch, 1787. In dem Plenck'schen Lehrbuche werden die verschiedenen zur damaligen Zeit bekannten Erkrankungsformen der Pflanze vollkommen denen des Menschenkörpers an die Seite gestellt. So werden behandelt die Wassersucht—*anasarca*—, die Auszehrung—*tabes*—, das Geschwür—*exulceratio*—, der feuchte Brand—*gangraena*—, die Laussucht—*phtiriasis*—, die Vollsaftigkeit—*polysarcia*—, der Baumkrebs als *carcinoma arborum* u.A.m. Bemerkenswert erscheint auch, dass Plenck seinem Lehrbuch eine *physiologia plantarum* vorausschickt. Er konnte das, denn er bekleidete nicht nur das Amt eines Doktors der Chirurgie sondern auch eine Professur für Botanik und ausserdem noch der Chemie.

Als Begründer der wissenschaftlichen Pflanzenpathologie in Deutschland darf Plenck aber doch nicht angesehen werden. Als solcher könnte weit eher der Göttinger Professor Persoon gelten, der in seinem 1797 erschienenen *"Tentamen dispositionis methodicae fungorum"* und erneut in der 1801 veröffentlichten *"Synopsis methodica fungorum"* die Urheber der Brand- und der Rostkrankheiten unter die Pilze einreihte. Der dadurch für die Pflanzenpathologie erzielte Gewinn war zunächst allerdings ein sehr bescheidener, immerhin war aber doch durch die Stellungnahme Persoons zu zweien der wichtigsten Pflanzenerkrankungen ein gangbarer Weg für wissenschaftliche Forschungsarbeit auf dem Gebiete der Pflanzenkrankheiten eröffnet worden. Die Wirrsale unter welchen Deutschland infolge der napoleonischen Kriege und ihrer Nachwehen zu leiden hatte, bewirkten, dass etwa erst vom Jahre 1830 ab erneut in die Bearbeitung pflanzenpathologischer Fragen eingetreten wurde. 1833 veröffentlichte Unger, wie Plenck, Doktor der Heilkunde, sein Buch über die "Exantheme der Pflanzen," in denen er nach Vorbemerkungen pflanzenphysiologischer Natur ausschliesslich pilzparasitäre Pflanzenkrankheiten abhandelt. Einen weiteren Schritt auf der von Persoon eröffneten Bahn tat Nees von Esenbeck mit seinem 1837 veröffentlichtem "System der Pilze." Auf ihn folgte nur wenige Jahre später, 1839, Wiegmann mit seinen sich vornehmlich an den praktischen Landwirt wendenden "Die Krankheiten und krankhaften Missbildungen der Gewächse," welches wissenschaftlich nicht viel Neues bringt, z.T. noch vollkommen in den Bahnen Plenck's wandelt. Mit dem 1841 erschienenen Werke von Meyen "Pflanzenpathologie. Lehre von dem kranken Leben und Bilden der Pflanzen," setzt für Deutschland eine Ruhe-Pause in der Bearbeitung phytopathologischer Angelegenheiten ein, welche dann etwa ein Dutzend Jahre später einer neuen Entwickelungsepoche Platz machte als deren Begründer deBary und Julius Kühn anzusehen sind. De Bary war anfänglich Mediziner später einer unserer verdienstvoltsten Botaniker, Kühn war Landwirt, aber Landwirt mit einem schar-

fen Blick für die wissenschaftliche Seite seines Berufes. Der neue Abschnitt pflan-
zenpathologischer Forschung wurde von Bary 1853 durch seine "Untersuchungen
über die Brandpilze," in denen allerdings Brande und Roste noch keine Tren-
nung erfahren haben, eröffnet; 1861 folgte die Abhandlung über "Die gegen-
wärtig herrschende Kartoffelkrankheit, ihre Ursache und ihre Verhütung; 1866"
"Neue Untersuchungen über die Uredineen;" 1867 und 1869 "Mitteilungen über
insektentötende Pilze." Ungeachtet dieses vielseitigen Eingreifens in pflanzen-
pathologische Forschung möchte ich doch nicht vorbehaltslos der vielfach ver-
breiteten Ansicht zustimmen, dass deBary für Deutschland als der alleinige
Begründer der neuzeitlichen Pflanzenpathologie angesprochen wird, wie das u.A.
Erwin F. *Smith* und *Duggar* tun. Ersterer mit den Worten: "Of all the person-
alities contributing to the advancement of plant pathology . . . . none has been
more interesting than that of deBary, none more productive of important results.
Und Duggar schreibt: "DeBary, who may be regarded as the Founder of modern
plant pathology."

Meine Stellungnahme stützt sich darauf, dass gleichzeitig mit deBary der
Begründer des Landwirtschaftlichen Institutes an der Universität Halle, Julius
Kühn, der pflanzenpathologischen Forschung in Deutschland neue und nach-
haltigste Anregungen gab. Kühn's Wirken unterschied sich von dem deBary's
dadurch, das er seine Forschungen in engster Anlehnung an denjenigen Zweig
der Volkswirtschaft, welcher ihrer am nötigsten bedurfte, ausführte, an die Land-
wirtschaft. In der Nutzbarmachung für das Volkswohl Deutschlands hat Julius
Kühn ganz unbestreitbar mehr erreicht als deBary. Bereits 1853 erschienen aus
der Feder Kühn's "Mitteilungen über die Krankheiten der Runkelrüben, denen
bald solche über den Rapsverderber *Sporidesmium exitiosum* folgten. Von
einschneidenster Bedeutung für die deutsche Pflanzenpathologie wurde aber
sein 1858 erschienenes, heute noch überaus wertvolles Buch "Die Krankheiten
der Kulturgewächse, ihre Ursache und ihre Verhütung." Es enthält die Ergeb-
nisse eigener Forschungen und ist bemerkenswert dadurch, dass es nicht nur
die pilzlichen Parasiten, sondern auch die tierischen und die nichtparasitären
Erkrankungen berücksichtigt. Bis in sein hohes Alter hinein hat sich Kühn der
pflanzenpathologischen Forschung gewidmet und ihr bleibende Werte zugeführt.
Herausgegriffen seien:

1. Der Nachweis von der Entstehung des Mutterkornes *Claviceps purpurea*.
2. Die Untersuchungen über das Eindringen der Keimfäden in die Wirts-
pflanze, besonders bei *Tilletia tritici*.
3. Die Prüfung des Verfahrens von Gülich zur Bekämpfung der Kartoffel-
krankheit.
4. Die Auffindung verschiedener neuer Pilzparsiten wie: *Tilletia secalis*,
Ustilago rabenhorstiana, *U. reiliana*, *Chrysomyxa albida*, *Calyptospora göpper-
tiana*, *Phoma hennebergii u.a.m.*
5. Die Auffindung der Nematoden *Tylenchus dipsaci* (später umbenannt
in *T. devastatrix*) und *T. havensteinii*.
6. Die langjährigen Untersuchungen über die Rübenmüdigkeit.
7. Beobachtungen über die Ueberwinterungsweise der Oscinislarven.

8. Die Auffindung einer neuen, auf dem Grase *Agrostis* Gallen erzeugenden Milbenart *Dendroptus krameri*.

Kühn war jedenfalls ein Pflanzenpathologe, welcher es vortrefflich verstand wissenschaftliche Forschung aus landwirtschaftlichem Bedarf heraus zu unternehmen. Er bewahrheitete, was Garman einmal ausgesprochen hat: science is pure, not withstanding, whether applied or not.

1874 trat Sorauer mit der Veröffentlichung seines "Handbuches der Pflanzenkrankheiten," 1880 Frank mit seinem Buch "Krankheiten der Pflanzen" in die Reihe der deutschen Phytopathologen ein. Sowohl Sorauer wie Frank haben eine reiche Forschertätigkeit entfaltet. Obwohl beide von Haus aus Botaniker waren, haben sie doch die Pflanzenpathologie in verschiedener Weise angefasst. Frank ist dabei Botaniker geblieben, Sorauer hat sich zum Pflanzenpathologen vom Fach verwandelt, wobei er aber nicht den Blick für die Grenzen seines Könnens als ursprünglicher Botaniker verlor. Sorauer führte die pflanzenpathologische Forschung auf eine neue Bahn, deren zielbewusste Verfolgung viel verspricht. Mit Sorauer endet der Abschnitt der ausschliesslichen Parasitensuche und beginnt die Lehre von der constitutionellen Vorempfänglichkeit, die Lehr von der Praedisposition, Resistenz, Immunität. Nicht dieser oder jener Parasit ist bei einer Erkrankung das Ausschlaggebende, sondern die Summe der durch Ausseneinwirkungen verschiedenster Art hervorgerufenen pysiologischen Vorgänge und Zustände im Pflanzenkörper.

Es muss zugegeben werden, dass das von Sorauer eröffnete Forschungsgebiet von ihm selbst nur eine Förderung von mässigem Umfange erfahren hat. Die Verantwortung dafür trägt nicht Sorauer sondern die Fülle der Schwierigkeiten, welche der Ergründung der jeweilig bestehenden Zustände im Pflanzenkörper entgegen stehen. Weder die Physik noch die Chemie sind bisher in der Lage gewesen, dem Pflanzenpathologen diejenigen feinen und feinsten Arbeitsmethoden zur Verfügung zu stellen, deren es bedarf, um die Wechselbeziehungen zwischen Zellplasma und Stofflösungen von ausserordentlich schwacher Konzentration, zwischen Zellplasma und schwächsten elektrischen, thermischen und solaren Einwirkungen in messbarer und damit vergleichbarer Weise auszudrücken.

Für die Forschungsrichtung Sorauers und für seine Auffassung vom Wesen der Phytopathologie ist es kennzeichnend, dass er in der 3. Auflage seines "Handbuches der Pflanzenkrankheiten" die Bearbeitung der parasitären Pilze und Tiere in fremde Hände gelegt, für sich aber die unparasitären, physiologischen Erkrankungen vorbehalten hat. Sorauer nähert sich damit dem Standpunkt, den Duggar (Phytopathology 1: 71. 1911) gelegentlich zum Ausdruck gebracht hat: the basis of the whole science (namely plant pathology) rests upon the foundation-stone of cellular irritability.

Eine weitausgreifende Förderung hat die Forschung alsdann durch die im Jahre 1898 erfolgte, auf eine Anregung von Julius Kühn zurückzuführende Errichtung der Biologischen Reichsanstalt für Land- und Forstwirtschaft erfahren. An ihr sind zahlreiche wissenschaftliche Untersuchungen ausgeführt worden. Sie auch nur dem Namen nach hier anzuführen müsste ermüden

wirken. Wenn ich an ihnen den kritischen Massstab anlegen sollte, so würde er zu dem Wunsche führen, dass das, wie gesagt sehr schwierige Gebiet der physiologischen Erkrankungen in Zukunft etwas stärkere Berücksichtigung finden möge. Die Erfüllung dieses Wunsches würde die Einstellung von Forschern, zur Voraussetzung haben welche über die Gesamtsumme des zur Lösung derartiger Fragen erforderlichen Wissens verfügen. Nach amerikanischem Vorbild hat die Biologische Reichsanstalt im Verlaufe der letzten Jahre eine Reihe von Zweigstellen (substations) eingerichtet. Ferner entsendet sie, ganz wie in den Vereinigten Staaten "fliegende Stationen" (Field agents) an Oertlichkeiten, woselbst irgend ein Kulturschädiger in seuchenhafter Weise auftritt. Gelegenheit zur Errichtung solcher fliegender Stationen bot in letzter Zeit der Koloradokäfer, die Rübenblattminierfliege und die Nonne. Neben der Biologischen Reichsanstalt bestehen in Deutschland noch einige selbständige Anstalten, welche sich ausschliesslich der wissenschaftlichen Bearbeitung von pflanzenpathologischen Fragen widmen. Es sind für Preussen: Versuchsanstalt Landsberg a. W.; für Bayern: Landesanstalt für Pflanzenbau und Pflanzenschutz in München; für Sachsen: Landwirtschaftliche Versuchsanstalt in Dresden; für Baden: Landwirtschaftliche Versuchsanstalt Augustenberg.

Endlich ist noch daraufhinzuweisen, dass verschiedene der von den Landwirtschaftskammern (farmer's incorporations) unterhaltenen Versuchsstationen mit Pflanzenpathologen besetzt sind, welche, soweit es ihre laufende Tätigkeit gestattet, ebenfalls wissenschaftliche Untersuchungen pflanzenpathologischer Natur ausführen.

Es sind zur Zeit drei Gebiete, auf denen in Deutschland eine rege Forschertätigkeit entwickelt wird. Sie lassen sich kennzeichnen durch die Worte: Immunität, Bodenreaktion, Samenstimulation. Alle drei Arbeitsgebiete sind bezeichnender weise unparasitärer Art. Sie greifen z.T. über das eigentliche Arbeitsgebiet der Pflanzenpathologie hinaus, versprechen dennoch aber für letztere von fühlbarem Nutzen zu werden.

Die Immunitätszüchtung liegt gegenwärtig noch fast volkommen in der Hand des Pflanzenzüchters, wird an einigen Stellen aber doch bereits in die Hand des Pflanzenpathologen hinüber geleitet z.B. an der Zweigstelle Naumburg der Biologischen Reichsanstalt.

Ob es jemals gelingen wird eine *unter allen Umständen* krankheitswiderständige Pflanzenabart auf dem Wege der Selektion oder Züchtung zu gewinnen, möchte ich bezweifeln. Dieser Zweifel stützt sich darauf, dass es nicht in unserer Macht liegt, gewisse Ausseneinflüsse, wie die Folgen der Düngungsweise, der Bodenbeschaffenheit, des Witterungsverlaufes so zu regeln, dass die angezüchtete Widerständigkeit in vollem Umfange zur Geltung gelangen kann. Damit soll indessen nicht etwa gesagt sein, dass die Immunitätszüchtung überflüssig ist. Es ist aber wünschenswert bei Zeiten auf die Schranken hinzuweisen, welche ihr von Natur ausgezogen sind. Bei uns in Deutschland ist u.A. K. O. Müller-Berlin dabei Sorten zu züchten, welche hinlängliche Widerständigkeit gegen *Phytophthora infestans*, *Synchytrium*, Rollkrankheit und Trockenheit besitzen. Seeliger-Naumburg versucht aus der reblausanfälligen *Vitis vinifera* Sorten

herauszuzüchten, welche reblausimmun sind. Roemer in Halle arbeitet an der
Züchtung rost- und brandfester Getreidesorten. Er machte dabei die Beobach-
tung dass Sporen von *Tilletia tritici* amerikanischer Herkunft nicht befähigt sind,
bestimmte deutsche Weizensorten zu verseuchen und dass umgekehrt gewisse
Weizensorten in den Vereinigten Staaten deutsche Tilletiasporen nicht annehmen.
Bei dieser Gelegenheit sei nicht unterlassen daraufhinzuweisen, dass sich die
Pflanzenpathologie im vorliegenden Falle eines über das der Humanmedizin
hinausgehenden Leistungsvermögens rühmen darf, denn es haben bisher noch
keinerlei Versuche unternommen werden können, bestimmten Krankheiten der
Menschheit, beispielsweise der Schlafsucht, auf dem Wege der Züchtung ent-
gegenzutreten.

Die Frage nach dem Zusammenhang zwischen Bodenreaktion und Pflanzen-
gesundheit hat die Heranziehung des Chemikers und des Elektrotechnikers
notwendig gemacht. Das bisher Erreichte kann keineswegs voll befriedigen.
Das Gleiche gilt von den Forschungen auf dem Gebiete der Samenstimulation.
Deutet auch Vieles daraufhin, dass zwischen Samenleistung und Pflanzengesund-
heit sehr enge Beziehungen bestehen, so muss doch zugestanden werden, dass
die bisher vorgelegten Forschungsergebnisse noch recht dürftiger Natur sind.
Trotz Allem darf gesagt werden, dass die deutsche Wissenschaft ungeachtet
der durch den Weltkrieg für sie geschaffenen schwierigen Lage auch auf pflan-
zenpathologischem Gebiete nicht müssig gewesen ist.

Indessen der Trieb zur Forschung würde in der heutigen Zeit wohl bald
erlahmen, wenn dem Errungenen nicht sehr bald die Nutzanwendung folgen
wollte. Es ist deshalb die Frage zu untersuchen, was tut Deutschland zur
Verwertung der nicht nur im Inlande sondern auch anderwärts erzielten For-
schungsergebnisse? In Betracht kommen hier hauptsächlich Männer, welche
Pflanzenpathologen vom Fach werden wollen und Landwirte, Gärtner und
Forstwirte. Je nachdem muss auch die Belehrungstätigkeit gehandhabt werden.
Wer sich heutigentages die Pflanzenpathologie zum alleinigen Beruf wählt, sei es
um später selbst Lehrtätigkeit auf diesem Gebiete auszuüben, sei es um die Rolle
des Beraters in pflanzenpathologischen Angelegenheiten, also die eines Pflan-
zenarztes zu übernehmen, der muss unbedingt die Morphologie, Anatomie und
Physiologie der Pflanze von Grund aus beherrschen lernen. Ausgerüstet mit
dieser Kenntnis und weiter mit allen den Kenntnissen, welche ihn befähigen das
sog. Ambiente der Pflanze übersehen zu können, soll er sich dann dem Pathologi-
schen zuwenden, so wie der Mediziner sein Studium mit der Einarbeitung in
gewisse naturwissenschaftliche Fächer, in die Morphologie, Anatomie und
Physiologie des Menschen beginnen muss und dann erst den kranken Körper
heranzieht für das Weitere.

Ganz anders liegen die Verhältnisse beim berufstätigen Landwirt. Er kann
nicht Pflanzenpathologe von Beruf sein und gleichwohl muss er Erkrankungen
seiner Kulturpflanzen zu verhüten und zu heilen verstehen, denn es fehlt zur
Zeit noch an der Einrichtung der Pflanzenärzte. Daraus entspringt für die
Pflanzenpathologie die Notwendigkeit dem Landwirte nicht nur die Ueberzeu-
gung von der grossen Schädlichkeit der Pflanzenerkrankungen beizubringen,

sondern ihm auch soviel pflanzenpathologische Kenntnisse, dass er in der Lage
ist gegebenfalles zielsicher eingreifen zu können. Der Landwirt muss mindestens
bis zur Stufe des Sanitäters herangebildet werden. Auf diesem Gebiete sind in
Deutschland im Verlaufe der letzten 20 Jahre erhebliche Fortschritte erzielt
worden. Die Pflanzenpathologie bildet zur Zeit einen mehr oder weniger umfang-
reichen Lehrgegenstand auf einer grossen Anzahl höherer Bildungsanstalten,
so an den Universitäten, an den Landwirtschaftlichen Hochschulen, an den
Forstakademien und den höheren gärtnerischen Lehranstalten.

Die ersten Vorlesungen an einer deutschen Universität wurden bereits im
Jahre 1864 und zwar von Julius Kühn in Halle unter dem Titel *de patologia
plantarum* abgehalten. Bereits vom Jahre 1863 ab veranstaltete Kühn ausserdem
pflanzenpathologische Uebungen, welche den Zweckverfolgten unter Hinzuzie-
hung des Mikroskopes und sonstiger Hilfsmittel dem in der Vorlesung Vor-
getragenen eine festere Grundlage zu geben. Die gleichen Einrichtungen bestehen
in Halle heute noch, sie sind aber mit Beginn des neuen Jahrhunderts in gross-
zügiger Weise ausgebaut worden. Die Zahl der gegenwärtig der Pflanzenpathologie
gewidmeten wöchentlichen Vorlesungsstunden beträgt 4, die Zahl der wöchent-
lichen Uebungsstunden gleichfalls 4. Die Uebungen haben eine Erweiterung
dadurch erfahren, dass neben den mikroskopischen Untersuchungen auch noch
die Herstellung, Beurteilung und Anwendung von Bekämpfungsmitteln erfolgt,
Diagnosen erkrankter Freilandpflanzen ausgeführt, Sämereien auf ihren Gesund-
heitszustand, Anschauungsversuche im freien Lande angelegt und Umschauen in
der Feldmark Halle gehalten werden. Die Zahl der an pflanzenpathologischen
Vorlesungen und Uebungen teilnehmenden Studierenden der Landwirtschaft
hat in Halle während der letzen 6 Jahre zwischen 230 und 280 geschwankt.
Die Pflanzenpathologie wird in Deutschland teils im Haupt- teils im Nebenfach,
gelehrt. Hauptfach ist sie an den Universitäten Halle, Hamburg, Kiel, München,
an den Hochschulen Berlin und Bonn-Hohenheim, an den höhern gärtnerischen
Lehranstalten Geisenheim und Dahlem. Hier werden sowohl während des
Winter als auch während des Sommerhalbjahres selbständige, das gesamte
Gebiet umfassende pflanzenpathologische Vorlesungen abgehalten. Die übliche
Einteilung des Stoffes ist dabei: parasitäre Erkrankungen im Winterhalbjahr,
physiologische Erkrankungen im Sommerhalbjahr. An den übrigen Lehrstätten
wird die Pflanzenpathologie als Nebenfach behandelt und jenachdem der
Zoologie, der Botanik oder der Pflanzenbaulehre eingefügt.

Die Einteilung des Lehrstoffes erfolgt dort, wo die Pflanzenpathologie im
Hauptfach gelehrt wird nach verschiedenen Gesichtspunkten, entweder werden
die Krankheiten und Schädiger der einzelnen Wirtspflanzen vorgeführt oder die
Darstellung erfolgt nach Schädigergruppen und dann im Anschluss an das
natürliche System. Für parasitäre Erkrankungen halte ich die Anordnung nach
den Krankheitserregern für zweckmässig, schon deshalb weil eine grosse Anzahl
von Parasiten sich nicht auf den Befall einer einzigen Wirtspflanze beschränkt.
Es sei nur an den Mehltau, an das Mutterkorn, an die Fusarien, die Roste, an
die Blattläuse, Nematoden und Milben erinnert, So steht bei *Erysiphe graminis*
das biologische Verhalten so sehr im Vordergrunde, dass demgegenüber die

Wirtspflanze eine ganz nebensächliche Rolle spielt. Für den Landwirt bietet jedenfalls der ihm bis dahin unbekannte Schädiger ein höheres Interesse als die ihm längst gewohnte Wirtspflanze des Schädigers. Ich habe beim Beginn meiner pflanzenpathologischen Lehrtätigkeit den Stoff nach Pflanzengruppen geordnet: Halmfrüchte, Gräser, Zuckerrübe, Knollengewächse, Leguminosen usw. bin aber dabei sehr bald inne geworden, dass die bei dieser Einteilung notwendigen Rückverweisungn auf schon einmal bei anderen Pflanzen erörterte Schädiger ermüdend wirkte.

Auch bei den Krankheiten physiologoscher Natur empfehle ich die Belehrung nach den Krankheitsanlässen vorzunehmen. Es wird dadurch möglich dem Lernenden die allgemeinen Gesichtspunkte für die Beurteilung der Krankheits-fälle fassbarer herauszuschälen. Einen geeigneten Weg hierfür hat Sorauer in seinem "Handbuch der Pflanzenkrankheiten" vorgezeignet. Er behandelt dort; 1 Ernährungsstörungen infolge von ungünstiger Bodenbeschaffenheit, von atmos-phärischen Einflüssen oder enzymatischen Misswirkungen; 2, Vergiftungen durch Gase oder Abwässer; 3, Verletzungen infolge von ungeeigneten Druckwir-kungen. Was endlich die nicht kleine Zahl der ihrer Ursache nach noch nicht erkannten physiologischen Erkrankungen anbelangt, so bleibt kaum etwas andere übrig als ihre Einordnung nach dem Krankheitsbilde, also: Rollkrank-heiten, Kräuselkrankheiten der Blätter, Mosaik, Chlorose usw. Lehrtätigkeit in gewissem Sinne üben auch die in Deutschland bestehenden Hauptstellen für Pflanzenschutz. Sie haben die Aufgabe dem Landwirte in Einzelfällen belehrend und beratend zur Seite zu stehen, ausserdem Beobachtungen über das Auftreten bestimmter Pflanzenerkrankungen zu machen. Deutschland ist zu diesem Zwecke in etwa 15 Gaue eingeteilt. Zusammen mit der Biologischen Reichsan-stalt bilden sie den "deutschen Pflanzenschutzdienst."

PROPOSAL FOR CO-ORDINATING RESEARCH ON THE
VIRUS DISEASES OF THE POTATO[1]

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In view of the urgent necessity, as shown by recent investigations, of a general reconsideration of the *Fusarium* problem, a conference of the *Fusarium* specialists of the Old and the New world was convened in August 1924 at the University of Wisconsin, in Madison. A similar revision of the problem of the degeneration diseases of the potato is no less a necessity. Pure cultures of the following diseases have been maintained for several years in the fields of the Institute for Phytopathology, Wageningen, Holland, and these plantings are continued every year, namely: (1) Leaf-roll, (2) mosaic, (3) crinkle, (4) stipple streak, (5) aucuba mosaic, (6) marginal leafrool, (7) interveinal mosaic, (8) coarse mosaic.

In America a nomenclature has developed which is largely independent of that of Europe, as the following list of diseases shows: (1) Leaf-roll, (2) mosaic, (3) yellow dwarf, (4) streak, (5) unmottled curly dwarf, (6) crinkle mosaic, (7) mild mosaic, (8) crinkle, (9) rugose mosaic, (10) spindling tuber, (11) leaf rolling mosaic, etc. International meetings have been held in order to establish a closer co-operation between all workers in this problem; in November, 1921, in London; in June, 1923, in Wageningen; but unfortunately the American specialists on virus diseases of potatoes did not attend these meetings. It is an urgent necessity that a new meeting should be held for the study, comparison, and identification of the virus diseases of the potato, in which the workers both of the Old and of the New world will take part.

The government of Czechoslovakia proposes to offer facilities for a Congress on Plant Pathology and Economic Entomology to be held in Prague, 1927. The official organisation of the Congress is at present delayed pending the recognition by the International Institute of Agriculture in Rome, which co-ordinates congresses in the field of science applied to Agriculture, of the International Committee appointed at the International Congress of Plant Pathology and Economic Entomology, Wageningen-Baarn, in 1923. If the Prague Congress materializes in 1927, it would be desirable that the American workers on the problem of virus diseases of potato should visit Holland and Ireland in passing through to Prague, in order to study pure types of European diseases, and to arrive, if possible, at a common understanding. The authors would be most pleased to facilitate the visitors in every possible way in their respective countries.

MYCOLOGICAL NOMENCLATURE IN RELATION
TO PLANT PATHOLOGY[1]

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Plant pathologists might justly inquire why they should be bothered with problems of mycological nomenclature. In reply it might be said that they would not be troubled with this matter if the mycologists had done their duty and settled it, as they should. Unfortunately, pathologists have to deal with fungous parasites for which they must have names. These names are mostly supplied and determined by mycologists. Now, as most of you know, the majority of plant parasites have from two to a half dozen or more names, due to over-zealous describers and namers of fungi.

The pathologist usually goes first to Saccardo for his names, or to some revious discussion of the disease he is studying. Unfortunately, but necessarily Saccardo's work is very imperfect and unsatisfactory for critical determinations. It is of course chiefly a compilation of the available and imperfect descriptions of fungi which are to be found in the much scattered mycological literature. It is self-evident that no person or small group of persons could be sufficiently familiar with the 70,000 to 80,000 fungi which have been described to determine their exact identity or synonomy. Saccardo undoubtedly did what he considered best under the circumstances in bringing together the great heterogeneous mass of names and descriptions and arranging them in a convenient manner for the use of mycologists. He did not hesitate to change, discard, or shift names to suit his ideas and scheme of classification. He necessarily made mistakes, but merely getting together in one series of volumes the great majority of names and descriptions of fungi was a large task and has been of much value and assistance to mycologists. Many species are of course described over and over again under different names and in different places because no critical study and determination of the synonomy could be made. Synonyms suggested by previous authors are frequently given. Used with a correct understanding of the purpose and limitations of the work it is extremely helpful, but if accepted as a final authority it is very misleading.

A thorough study of any group of species shows that the same parasite is masquerading under different names, not only in Saccardo but in other systematic works on the fungi. We are only just beginning to realize how numerous and confusing these cases are and what serious mistakes they may cause. The determination of the vast synonomy in taxonomic mycology is a problem re-

[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 18, 1926.

quiring the services of thoroughly trained and well-equipped taxonomists. As these synonyms become known the question arises as to which of the various names that have been applied to the plant shall be used. Present rules generally require the adoption of the oldest name. This, however, is frequently the least known name and its adoption necessitates discarding the one with which we are most familiar. If this single change ended the matter we might possibly submit to the trouble and inconvenience caused, but very frequently it is later discovered that there are still older names which have been overlooked, and we must continue to make changes until the last one has been discovered, the result being that instead of stability and uniformity this plan requires more or less frequent and indefinite change. When mycologists were few and pathologists and other workers in economic mycology had not yet appeared, changes of names did not affect many people. Conditions are very different now, with hundreds of people using plant names where one used them before.

The failure of the priority plan to secure a reasonable degree of stability and uniformity in the use of names has raised the question as to whether these ends can not be more easily and quickly attained by some other method. For the majority of important parasitic fungi there are names which have at present rather wide general usage. Why not then make these names permanent instead of changing them every time an older one is found? This would seem rational and I believe it is practicable.

To carry out this plan it would be desirable to have a competent committee prepare a list of genera and species selected on the basis of general usage and have these names definitely fixed by assigning nomenclatorial types to them. Such a standard list of names when prepared should be made available to all and used by all. The time seems to have arrived when all persons and groups who must use technical plant names for scientific and practical purposes should take an intelligent and active interest in this subject and help to secure as quickly as possible reasonably stable and uniform names, at least for our most important economic species, both hosts and parasites.

That the plan we have outlined is regarded by others as feasible is attested by the fact that it was unanimously approved by the Plant Physiology Section of the Botanical Society of America at the Kansas City meeting, and has also been endorsed by twenty or more well-known botanists to whom it has been submitted individually.

AN INTERNATIONAL PLANT HEALTH LEAGUE:
A PROPOSAL[1]

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A large number of persons in all parts of the world are interested in the improvement of crops and of crop yields by means of immune or disease-resistant varieties.

These persons are not now united in any single organization or bond of mutual helpfulness, but on the contrary from choice and training are to be found in various societies—horticultural, agronomic, pathologic, botanic, etc. It is believed that the number of persons having this common interest is sufficiently large to justify the formation of an organization which would prove most beneficial to the members without imposing any financial hardship or onerous duties on any member.

All workers hope to reach the stage when their creations may be distributed to any scientist who cares to have them. It frequently happens too, that plant workers find or have available plants exhibiting immunity or resistance to disease with which they have no desire or opportunity to work. In another part of the world there may be an individual who would be very glad of the opportunity to make use of the plants in his work. In other cases severe tests for immunity can not be secured because the infecting organism does not make its appearance early enough or often enough. Authentic cultures of the organism involved might be secured and used for inoculation if one only knew where to turn quickly to secure the culture.

Discrepancies in results between two widely separated workers might be studied and explained by friendly cooperation rather than complicated by indulgence in polemics.

Biological specialization among the pathogenes or among the hosts is a well established fact. Variety testing under a wide diversity of conditions, therefore, becomes of great importance and constitutes a type of work which might well be fostered by those persons who are most concerned.

An increased interest in this type of work might have a far reaching effect in many directions. Elimination of the disease factor in crop production would have a tendency to stabilize any plant industry and help to reduce existing fluctuations in yield and price. In the same way a variety might be found which proved resistant to a serious disease in all parts of the world. Restrictive measures might then be removed with entire safety and thus another tiny source

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[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 18, 1928.

of international discord could be abolished. The funds now used in enforcing quarantine regulations then could be diverted to more profitable channels and it is conceivable that the time might come when there would be no scientific basis for the maintenance of such administrative officers.

The cost of maintaining such an organization would be very small indeed. There is no occasion to establish elaborate machinery for operating the league. The league must stand or fall upon mutual good will and cooperation between individuals. In its simplest and perhaps best form, the labor involved would consist in compiling and distributing once each year an address list of the members with a statement of what each member has to offer and of what he desires. The further functioning of the league would then become a personal matter between interested individuals.

On this basis the annual expense for each member would consist in the cost of two postage stamps and his proportionate share in the printing or mimeographing of about 100 copies of a leaflet of perhaps 4 or 6 pages.

In addition, the officers of the league might find it possible to facilitate inspection of material intended for members of the league and thus eliminate a source of delay and annoyance which has proved most exasperating in numerous instances.

It is possible that formal organization is not necessary, for this type of exchange already is going on all the time. It does seem, however, that a member of the league might have less hesitation about asking a fellow-member for experimental material than he otherwise would have, and certainly the annual exchange of desiderata and offering lists would stimulate an even wider interchange of plant materials than exists at present.

On the above basis I, therefore, propose that those persons present at this Congress who are interested constitute themselves an organizing committee to form an International league for permanent crop improvement through the development of disease resistance and I present the following simple constitution as a working basis for such an organization.

INTERNATIONAL LEAGUE FOR PERMANENT CROP IMPROVEMENT THROUGH DEVELOPMENT OF DISEASE RESISTANCE

Constitution
ARTICLE I
Name

This organization shall be known as the International League for Permanent Crop Improvement through Development of Disease Resistance.

ARTICLE II
Membership

Sec. 1. The organization shall consist of members, and may include life members and patrons.

Sec. 2. Each member shall pay annually or at longer intervals such dues as the League shall determine.

Sec. 3. Any member may become a life member upon the payment of $50.

Sec. 4. Any person may become a patron upon the payment of $200., and upon election may become a member of the League.

ARTICLE III

Eligibility and Election of Members

Sec. 1. Any person is eligible to membership who is actively and scientifically engaged in crop plant improvement through the development of immune or disease resistant varieties, or who is interested in the fundamental problems of immunity and disease resistance in any of its phases.

Sec. 2. Any person elects himself to membership in the League by formally notifying the General Secetary-treasurer that he desires to become a member and that he is eligible as indicated in Sec. 1 of this article.

ARTICLE IV

Officers

Sec. 1. The officers of the League shall consist of a general secretary-treasurer and a secretary-treasurer for each national group of members. Their duties shall be those usually performed by such officers.

Sec. 2. The several secretaries, with the general secretary as chairman, shall constitute an executive committee. All actions of the executive committee must be authorized or approved by the membership.

Sec. 3. Temporary or standing committees may be appointed at the discretion of the League.

ARTICLE V

Meeting

Meetings of the League or of national groups may be held when desirable and at such time and place as the council may designate.

ARTICLE VI

Election of Officers

An organizing committee shall select officers to serve for the first year. Thereafter the general secretary-treasurer shall submit to each member two ballots, one for general secretary-treasurer and one for national secretary-treasurer. He shall canvass the ballots six months from date of their issue and shall declare that member elected who shall have received a plurality vote.

ARTICLE VII

Amendment

This constitution or its by-laws may be amended at any time by a majority vote by ballot, of the members.

By-Laws

The general secretary shall notify all members at least 6 months in advance of an international meeting.

The national secretary shall notify his members at least 1 month in advance of a national meeting.

The general secretary shall circularize the entire membership, either directly or through the national secretaries as may be determined in each individual case, each year calling for (1) a list of offerings and a list of desiderata, (2) for general proposals looking to the improvement of the League, (3) for amendments, etc., etc. The information so gathered shall be distributed by the general secretary-treasurer at the earliest possible date after replies could reasonably be expected. The secretary shall time his inquiries and summaries in such a way as to avoid if possible the loss of a crop year as between northern and southern hemispheres.

The secretary-treasurer shall levy an initial assessment on each member of $1.00, or equivalent with the expectation that an additional levy shall not be made for several years.

Active members shall consist of those individuals who pay the assessment and who answer the annual questionnaire with promptness.

THE NATURE OF MOSAIC DISEASES[1]

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In any discussion of the nature of the causal agency producing mosaic diseases it should be clearly stated at the outset that we are far from prepared to make an announcement that might seem to have the appearance of finality. There is a vast array of observations concerning the appearance and behavior of mosaics, and while the great majority of these records throw little light on the nature of the agencies at work to produce the characteristic symptoms of these well known diseases, there are groups of observations that seem to constitute most important links in the yet imperfect chain of evidence which, when more nearly complete, may enable us definitely to infer the nature of these infectious agencies.

In this brief review, sketchy consideration of new data, and tentative outlook, it will not be possible for me to examine, or even list, all the evidence for or against any particular view. At the risk of being judged dogmatic, I must exclude from this discussion all that seems to me inessential in focusing attention upon the nature and properties of mosaic agencies. Further, it will be helpful to have in mind chiefly those mosaics that are commonly considered typical. By typical I refer, of course, to that type of infectious mottling or variegation of leaves generally characterized by the presence of irregular areas of deeper green and of paler green (or green and yellow green) associated with deep-seated differences in the histology of the leaf blades. This characterization is unsatisfying, but it will perhaps suffice if I illustrate by mentioning as examples the ordinary mosaic of tobacco, cucumber mosaic, bean mosaic, and mosaic of corn and sugar cane. There are undoubtedly hundreds of hosts for such typical and readily transmissible forms of the diseases under discussion. For the moment we may disregard how close or how distant may be the relation between typical mosaics and those infectious agencies of plants in which a more general yellowing prevails. Likewise, we need not now raise the question of including "infectious variegations," and far less the various chlorophyll deficiency "diseases."

In referring to those typical mosaic diseases as virus diseases, no exclusion of the other classes is intended, nor is it to be inferred that there is necessarily any closer relation of the former with the virus diseases of animals. This problem is simply not considered at the present time. Indeed, from MacCallum's recent review, "Present knowledge of filterable viruses," one would, I think, logically conclude that there is both great diversity of behavior and no little confusion as

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[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 18, 1928.

to specificity and relationships in respect to animal forms. Among the points of resemblance between plant and animal virus disease agencies, the important ones are, practically speaking, included in the very definition of the group; infectiousness, ultramicroscopic size often inferred rather than determined, and the quality of being not amenable to cultivation—*in vitro*. To a very large extent both groups display, in the invaded tissues, certain accompanying intracellular (or intranuclear) bodies.

The observations on which we may base any suggestions concerning the nature of mosaics are primarily of two types. The one is largely cytological, and this, by carefully portraying the comparative appearance of diseased and healthy cells, has yielded evidence of great diagnostic value and of some presumptive etiological significance. Recent work along cytological lines has been particularly suggestive in respect to the intracellular bodies. So far as studied in plants, these bodies are fairly uniform in appearance, relatively large, and should be readily amenable to microchemical study. Some few investigators on the plant side seem still to view these bodies as organisms with certain characteristics of other known forms. The evidence is purely cytological, full of anomalies even in that regard, and does not accord with the experimental facts. Detailed cytological work is most important, however, although final proof concerning the etiology of the infectious agency and behavior studies to determine the nature of this agency are necessarily dependent upon experimental work of extremely varied types. It is not a simple problem experimentally, and perhaps it is not to be expected that all cytologists will be willing to interpret their finding with regard for the experimental evidence, much less will they convince themselves by instituting experiments.

Looking backward to the work of Beijerinck on tobacco mosaic, and his suggestion of a "living fluid"—the prototype of all viruses—there have been various theories concerning the nature of the agencies in mosaic diseases. It is unnecessary here to discuss them further than to say that, in general, beginning with protozoa and passing on through bacteria, enzymes, and chemical compounds of undefined characteristics, we have briefly the relationships that have been assigned by different investigators. About a score of persons have expressed the view at one time or another that the causal agent in any given case is a visible living organism with affinities among known forms. These views began with the work of Iwanowski (1903) and the most recent are those of Klebahn (1925) and of Eckerson (1926). However, among those who have held or are holding the view that microscopic organisms are the causal agencies, there is no morphological agreement, except in so far as several infer the causal nature of the intracellular bodies. This careful grounding of viewpoints on cytological and morphological evidence should not be confused with much "interpretative" writing. In the latter the case for mosaics is all too frequently stated for the non-specialist in plant pathology somewhat as follows: 'The causal organism is not definitely known, but the invisible agency acts in all respects like bacteria.' Such statements are most unfortunate.

It is particularly interesting to note that in the recent work on intracellular bodies, especially that of Miss Smith (in press at this date), it has been found

that these structures in tobacco mosaic are confined in their distribution to the paler or hypoplastic areas, so far as the leaf is concerned. It is significant that the distribution of the virus does not appear to be confined to such areas. In my preliminary experiments with virus distribution in these contrasting areas a careful endeavor has been made to dissect out small masses of the deeper green tissues, and similarly small masses from the yellower, areas, inoculations being subsequently made in the usual manner. In the dissection work every possible precaution has been taken to prevent contamination. It can not be stated definitely that islets of hypoplastic tissue may not occur in some of the deeper green areas. However, it does seem that differential results in inoculation should be possible by this method. With undiluted juices from diseased leaves we have been able to distinguish no differences in the infectiousness of such tissues. Naturally the problem of the relative concentration of the virus, quantitatively, will require a special technique. Nevertheless, the indications from these results as well from others to be enumerated, are that the protoplasmic bodies may not be even closely related to the distribution of the virus, and accordingly must be regarded as secondary effects.

I have just referred to the distribution of the virus in the different areas of the mottled leaf,[2] and it should be further emphasized that the evidence at present is that there is a general distribution of the virus in the host. From the work of Allard it would appear definite that this may indicate its existence in all tissues excepting those of the developing seed. Confirming earlier work, my experiments have shown that from a single point of inoculation in a half-grown tobacco plant this distribution to all the tissues may occur within a period of about five days under the most favorable conditions. This is truly remarkable when one bears in mind the absence of general circulatory fluids in plants. A second established relationship is that of the relatively high resistance of this disease agency to temperature and such chemical agents as acids, alcohols, salts of the heavy metals, etc. This relationship places the agency, in respect to inactivation or "killing" in a class parallel with enzymes, certain spores, and some of the more resistant vegetative cells.

It will be obvious that experimental studies of such virus diseases necessarily proceed slowly, involving in every instance infection experiments with the host, since by that means alone (that is, the results of infection experiments) can we know the effect of any treatment or behavior study.

Little is known concerning the details of the process of infection. The part which the tobacco aphid (*Macrosiphum tabaci*) plays in "natural" infection has been demonstrated apparently, and artificial infection through any wounds, especially by needle pricks, with the tiniest drop of diseased juice yields nearly 100 per cent of positive cases. But there is a striking lack of evidence regarding the activity or motility of the agency in relation to disease production. There is little if any evidence that the virus may enter the living cells unless the tissue is injured to the extent of wounding the cell, or at least effecting a separation of adjacent cells. The probability seems to be that the virus must actually be placed

[2] Unless otherwise stated, all references in this paper to the special work of others, or to experimental work here reported, are in respect to the mosaic disease of tobacco.

in the injured cell or at least in contact with the plasmic connections, the plasmodesmen, between adjacent cells. Infection is invariably a function of cell disturbance, a gross scalpel cut is less effective as a means of entry than many fine needle pricks.

Attempts to induce the disease by infection through the stomata or by spraying the virus on uninjured leaf surfaces containing few stomata have not thus far given consistent results. Generally surface spraying does not lead to infection, but in one case the incidence of infection was as high as 50 per cent. It seems scarcely possible that injuries could have accounted for this result. On the other hand, many experiments have been negative. Likewise, the location of waterholding chambers (of the live-chamber type) on the leaf, prepared in such manner that juice from infected plants was kept in contact with the uninjured leaf surface for twenty-four hours, yielded only one infection in thirty trials. Obviously this requires special study in relation to stomatal opening, and perhaps in pure culture as a precaution against wounds. Under certain conditions, then, the virus would seem to have no more effect than inert particles, yet when introduced into immediate contact with, or into, diseased or injured cells it passes through the plants with amazing rapidity.

After a consideration of much of the work that had been done up to that time on the intracellular bodies, it seemed to me some years ago that a most fruitful line of experimentation would be that of determining with some degree of certainty the filterability of the tobacco virus under rather diverse conditions. A first report on those studies has been published (Duggar and Armstrong). Using standardized filters and employing the most careful bacteriological technique it has resulted invariably that the agency of the mosaic disease of tobacco is found to pass readily through porcelain filters and with a time interval corresponding very closely to that of 1 per cent hemoglobin, though somewhat less freely. The more recent work has been directed toward a study of the conditions affecting filterability. In general, I may say that this mosaic agency passes through all of the standard commercial filters, whether made from porcelain, diatomaceous earth, gypsum, or other materials of this general type. Moreover, we have been able to dilute it markedly and in reasonable time by filtration with one type of filter only. This filter is one of the early forms of cylindrical porcelain atmometers. From such results, repeated many times, it has been determined that the tobacco mosaic agency may exist in the form of a particle 30 to $35\mu\mu$ in diameter. This size is reckoned, however, by comparison with hemoglobin after the work of Bechhold, and it has not yet been possible to consider any more recent studies. It should be stated here that no independent attempt to determine the size of the particles of the tobacco virus has been made, so far as I am aware. It will be seen that this particle size is beyond microscopic vision, even with highest powers, and perhaps places the agency in the class of a large group of complex organic substances.

Criticisms against filtration methods are based primarily upon two possibilities: first, a failure to give correct size because of precipitation in the pores of the filter, and second, the passage of relatively large particles owing to defects

in the filter, which may permit particles actually much larger than those calcu-
lated to pass through. With respect to the first type of criticism, I think all
would agree that it is justified to a certain extent but I have been able to use
filters of different types in which the charge on the pores against water is differ-
ent. Again, I have placed the diseased juice containing the virus in buffers
ranging from pH 3 to pH 9, therefore filtering under conditions in which hydrogen
ions are in large excess, hydroxyl ions in large excess, as well as under conditions
of practically equal concentration of H and OH ions. The juice of the tobacco
plant is ordinarily about pH 5.5 to 6.1. Under the various conditions mentioned

TABLE 1. FILTRATION OF BACTERIA
(A plus sign indicates the ability of the organisms to pass the filter and a minus sign denotes that they are withheld)

Organism	Filters and culture media											
	Spherical				Chamb. B.				Cyl. Atm.			
	F.a	O.a	Bo	L.m	F.a	O.a	Bo	L.m	F.a	O.a	Bo	L.m
Azotobacter vinelandii I	−	−	−	−	−	−	−	−	−	−	−	−
Azotobacter vinelandii II	−	−	−	−	−	−	−	−	−	−	−	−
Bacillus prodigiosus	+	+	+	+	−	−	−	−	−	−	−	−
Bacillus coli	+	+	+		−	−	−		−	−	−	−
Bacillus mycoides			−	−			−	−			−	−
Bacillus megatherium	−	−	−	−	−	−	−	−	−	−	−	−
Bacillus subtilis	−	−	−	−	−	−	−	−	−	−	−	−
Bacillus radicicola	−	−	−			−	−	−		−	−	−
Bacterium atrosepticum	+	+	+		−	−	−		−	−	−	
Proteus vulgaris			+	+			−	−			−	−
Pseudomonas tumefaciens	+	+	+	+	−	−	−	−	−	−	−	−
Sarcina flava	−	−		−	−	−		−	−	−		−

Cultures described as follows: F.a = fresh agar slants; O.a = agar slants one month old; Bo = fresh bouillion; L.m = Löhnis medium.

the mosaic agency passes the finest porcelain filter employed, whether or not
final precipitation and clogging of the pores may result. In respect to the second
point, that of defectiveness of the filter, the criticism is a natural one, at least on
the part of the plant pathologist. He is primarily concerned with the larger
parasitic forms and he questions the care that may be given and the accuracy
that may be employed in filtration work generally. Fortunately, if there is any
inaccuracy in such work, whether arising from filter defects or from faulty
technique, it must become evident when the same filters and the same technique
are employed with bacteria, for with such organisms the passage of a single cell
through a defective filter candle may be determined by subsequent culture work.

In some studies designed to throw light upon the life cycles of the bacteria I have, with the assistance of Mrs. E. P. Miller and others, tested extensively these possibilities of larger organisms passing the kind of filters employed in mosaic work.

For comparison I have used a graded series of filters: the most porous, spherical atmometer cup 16–2, permitting certain bacteria to pass; a Chamberland B candle, holding back all bacteria thus far tested but allowing free passage of the mosaic agency; and a cylindrical, porcelain atmometer cup of the type originally used in our work. The latter dilutes somewhat the mosaic virus. In this work the utmost precautions were taken, and precisely the same precautions were used in the mosaic experiments.

TABLE 2. INOCULATION EXPERIMENTS WITH FINELY GROUND MATERIAL
FROM DISEASED TOBACCO LEAVES

Treatment	No. plants	Total diseased after 3 weeks
Ground 3 hours......................	10	8 plants diseased
Ground 9 hours......................	10	6 plants diseased
Control, no inoculation...............	10	None diseased
Control, fresh dis'd. juice in diatomaceous earth.........................	10	7 diseased

TABLE 3. EFFECT OF GRINDING WITH DIATOMACEOUS EARTH ON INFECTIVITY OF DISEASED JUICE

Treatment	No. plants	Total diseased, after 18 days	Per cent diseased
Control, diseased juice+diatom. earth	20	18	90
Ground 3 hours	20	18	90
Ground 6 hours	20	18	90
Ground 9 hours	20	17	85

TABLE 4. EFFECT OF GRINDING ON THE INFECTIVITY OF DISEASED LEAF MATERIAL OF TOBACCO

Treatment	No. plants	Total diseased after 21 days	Per cent diseased
Control	20	19	95
Ground 3 hours	20	20	100
Ground 6 hours	20	20	100
Ground 12 hours	20	20	100

Finally, in relation to filtration studies, tests have been made in which the diseased tobacco juice was mixed with cultures of bacteria and a sample of this mixture subjected to filtration under exactly the same conditions as those previously described. I shall indicate the results when the diseased juice was used in connection with *Bacillus prodigiosus*. The filterability of this *Bacillus* was determined by plating samples of the filtrate, and that of the virus in the usual inoculation tests. Filtration was carried out at a pressure of about one-third atmosphere, using the cylindrical atmometer cup already described, 6cc. of filtrate being secured in one hour.

The original count of the bacteria in the sample to be filtered was 2,080,000 per cc. Plates made from 1 cc. samples of the filtrate remained perfectly sterile. Of ten plants inoculated with the unfiltered mixture, nine became diseased within the appropriate period, while a similar number of inoculations with the filtered juice yielded seven plants affected with mosaic. Confidence in the capacity of the filters to hold back any larger organism seems wholly justified.

Through experiments already reported in part it has been shown that the usual procedure of grinding with diatomaceous earth does not readily affect the infectivity of the mosaic virus. Grinding was effected in an agate mortar provided with a motor-driven, excentrically arranged pestle, a device frequently employed in grinding bacterial cultures. In one case reported the procedure has been as follows: The diseased leaf material was pulped by passing it through a meat grinder, and then, after removal of the coarser parts, ground in a hand mortar, and finally there was added an equal weight of diatomaceous earth, and the final grinding given. The results are shown in table 2. The fact that the inoculation experiments do not yield as high a percentage of infections as usual may be due in part to the use of older plants and possibly in part to adsorption action of the diatomaceous earth, as further discussed later in this paper.

In a recent experiment the treatment was somewhat different. The diseased leaf material was pulped in a mortar, and all the coarser particles filtered off through absorbent cotton. This undiluted juice was mixed with diatomaceous earth in the proportion of one part of the silicious earth to three parts of juice. This mixture, protected from contamination, was dried, and then ground for varying periods as shown in table 3. The control mentioned is the same material not subjected to grinding.

Another example of the effect of grinding may be given in which the procedure was somewhat different. In this case the diseased leaves were dried, then pulverized in a mortar and finally sieved. It was mixed with diatomaceous earth in the proportion of 5 grams of the dried leaves to 7.5 grams of siliceous earth. The ground and unground (for control) powder was in each case made sufficiently fluid by the addition of 11 cc. of water to each gram of the material, and inoculations were made as usual. Table 4 gives the final results.

Previously there has been a brief description of grinding experiments with *Bacillus subtilis*. These should, for comparison, be given in more detail and are presented in table 5.

In addition to the experiments just described I shall refer to a test of this method of grinding as applied to the smaller but non-sporeforming *Bacillus* (*Erythrobacillus*) *prodigiosus*.

A heavy broth culture of this organism (10 cc.) was mixed with approximately $3\frac{1}{3}$ grams of sterile diatomaceous earth in a sterile Petri dish and allowed to dry 4 days at room temperature, with the lid of the Petri dish supported on glass rods so as to allow the water vapor to diffuse out. The dried material was then scraped up with a sterile spatula and put in the mortar of the grinding machine. In order to render the apparatus relatively sterile the mortar and pestle had been soaked in 8 per cent formaldehyde for 15 minutes, then rinsed in 95 per cent

alcohol, and the residual alcohol burned off. During grinding it was shielded from dust as far as practicable.

A sample before grinding was removed to a sterile Petri dish; likewise samples were removed after $1\frac{1}{2}$, 3, and $4\frac{1}{2}$ hours' grinding. A sample of 0.2 gm. was weighed out from each of these and plated, in the usual way.

TABLE 5. GRINDING EXPERIMENTS WITH BACILLUS SUBTILIS IN SPORE CONDITION

Time of grinding	Dilution	Plate	Number of colonies
3 hours	$1-10^2$	1 2	64 0
	$1-10^3$	1 2	3 1
	$1-10^4$	1 2	0 0
	$1-10^6$	1	0
6 hours	$1-10^2$	1 2	1 2
	$1-10^3$	1 2	0 0
	$1-10^4$	1 2	0 0
	$1-10^5$	1 2	0 0
	$1-10^6$	1 2	0 0
9 hours	$1-10^2$	1 2	0 0
	$1-10^3$	1 2	0 0
	$1-10^4$	1 2	0 0
	$1-10^5$	1 2	0 0
	$1-10^6$	1 2	0 0
Unground	$1-10^4$	1 2	640 800
	$1-10^5$	1	208
	$1-10^6$	1	140

The results of the grinding experiments are incompatible with the view that an organism of the usual characteristics, or any organism of microscopic dimensions may be causally related to the tobacco mosaic.

The next major line of investigation which seems to throw some light upon the characteristics of the disease agency is that of the effect of the juices of other plants. I have utilized thus far the juices of about one dozen plants, three of which have proved more or less injurious to the mosaic virus. I shall concentrate attention upon the juice of the poke weed. If the diseased tobacco juice is mixed with healthy poke weed juice in any quantity in which the ratio is not greater than 1:2 the infectivity of the tobacco juice is completely annihilated, or inactivated. When, however, the quantity of the diseased tobacco juice is greater than that of the poke weed juice, the incidence of infection depends upon the relative amounts employed, poke weed juice being wholly ineffective when five times as much diseased tobacco juice is used. Many other experiments have

TABLE 6. GRINDING EXPERIMENTS WITH BACILLUS PRODIGIOSUS

Treatment	Plate count, 0.2 gm. material	Plate count per gram
Unground	10,700	53,500
Ground $1\frac{1}{2}$ hours	70	350
Ground 3 hours	Sterile	0
Ground $4\frac{1}{2}$ hours	Sterile	0

been made but we have not thus far been able to recover consistently the disease inducing agency from the poke weed matrix. Nevertheless, there are many indications that we are dealing in large part with a problem of adsorption. The poke weed juice is ineffective as an injurious agent toward plant cells in general and toward microorganisms. The filtration of the juice through porcelain filters reduces notably its effect toward the mosaic virus. This problem is under careful investigation and it is hoped that a method of procedure may be developed whereby any possible specific toxic effect of the juice may be discovered.

In an attempt to study the behavior of the mosaic virus in the presence of substances that might act as adsorbents some preliminary work has been done. Earlier results had indicated that in such work more consistent data may be expected if the virus is diluted, or if it is filtered through some one of the coarser filter candles. In the experiments outlined in table 7 juice from diseased plants, diluted with an equal amount of water, was permitted to stand several hours, during which time coarser materials settled out. It was then centrifuged at about 2500 revolutions per minute for five minutes, and finally filtered through a spherical atmometer cup. The various agents were allowed to act from 12 to 15 hours. Inoculations were then made, distilled water being first added in experiments 5–8 so that each was sufficiently fluid to be "worked in" conveniently with the needle.

These experiments would seem to emphasize the adsorption relations of the virus. Admitting some apparent injury from the effects of the dibasic sodium phosphate, probably from its alkalinity, we find that the addition of $CaCl_2$,

in itself without effect, gives a precipitate which, under these conditions, carries down the virus. The filtrate contains less of the virus than could be predicted, while the residue not only contains the virus, but would seem to set it free upon inoculation, probably due to the solution of the residue. Precipitated $CaCO_3$ is active in reducing the efficiency of the virus either by alkalinity or by adsorption. Charcoal, a highly adsorbent and at the same time oxidizing agent, is wholly efficient in rendering the mosaic agency inactive. It should be stated that the charcoal used in the above experiment was first wetted and washed with alcohol, then subsequently washed three times with distilled water. In this condition the charcoal is non-injurious to *Micrococcus prodigiosus, Aspergillus niger*, and other readily culturable organisms. The effect of charcoal is to be made the

TABLE 7. EFFECT OF CERTAIN PRECIPITATING OR ADSORBING

Treatment	Number of Plants	Total number of plants diseased, after			Percentage diseased
		7 days	9 days	16 days	
1. Control, diseased juice	10	5	9	9	90
2. Diseased juice in m/20 Na₂HPO₄	20	1	5	7	35
3. Diseased juice in m/20 CaCl₂	20	16	18	18	90
4. Diseased juice in Na₂HPO₄+CaCl₂, filtrate	20	0	0	1	5
5. Diseased juice in Na₂HPO₄+CaCl₂, residue	20	9	15	16	80
6. Diseased juice in diatomaceous earth, 3cc. to 1 gm.	20	8	15	15	75
7. Diseased juice in precipitated CaCO₃, 3 cc. to 1 gm.	20	4	8	10	50
8. Diseased juice in blood charcoal, 5 cc. to 1 gm.	20	0	0	0	0

basis of a special report when further work is completed. That adsorption may be an important factor in the process is further suggested by the rather diverse behavior of different animal and plant charcoal preparations, which I cannot discuss at this time.

Considering the definite results yielded by these three lines of experimentation, that is, filtration, mechanical grinding, and adsorption or other effects of certain solid agents, I am forced to the conclusion that the infectious agency is a particle of almost inconceivably small size, certainly too small to represent an organism with the usual characteristics. In making this suggestion I must, of course, abandon earlier views, but the idea is in full accord with statements I have made at several botanical meetings during the past winter.

The filtration studies suggest an agency too small for an organism endowed with endometabolism, though space does not permit of a presentation of the reasons therefor. On the basis of the grinding experiments, or mechanical comminution, we have at least a qualitative indication of ultramicroscopic size.

No large organism can be logically pictured that would resist this process as carried out in the excentric mortar during a time interval far greater than is required to rupture the cells of bacteria, both spore and vegetative units. Whether one pictures the hypothetical organism as an extremely attenuate thread or as a highly fluid body, grinding should effect complete disintegration.

The third line of evidence, that in which adsorption relations may play a rôle, yields thus far no accurate measure of size relations, of course, but at the present time, and in spite of oxidation possibilities, I am disposed to interpret the solid-agent work and the action of poke weed juice as emphasizing an adsorptive capacity, in any case pointing clearly to very minute size. On the other hand, I find these results a direct refutation of any view advocating a causal organism of protozoan dimensions. The filtration and grinding experiments indicate that minute particles are concerned, the adsorption experiments suggest that large particles are not concerned. So far as these physical and mechanical experiments have gone we have the strongest evidence for the colloidal behavior of the agency concerned.

The difficulty in conceiving of this disease agency as anything but a living organism of the usual type is due chiefly, I think, to the indefiniteness with which we are then faced. We know that the virus has the power of multiplication within the host, and this capacity for reproduction, in general, is associated with a living organism, and along with this capacity there are other properties which seem to satisfy the requirements of many criteria of life, such criteria as might seem properly to apply to theoretically simple life.

Summarizing, it appears that with the facts already reviewed we must either consider that this virus is not a living thing at all or that it constitutes a kind of living thing of which we have had previously no very definite conception, unless the extensive work on the basteriophage may be considered analogous.

To satisfy the experiments presented, it would seem almost necessary to assume a low order of correlation, since this would be the only possibility in a body of colloidal dimensions. The other alternative is the assumption of a chemical substance capable of stimulating the protoplasm of the infected host to reproduce the same material, an assumption that has been made twice or three times earlier; but this is an assumption which has as a basis, it would seem to me, far more uncertain analogies.

I can only look upon this problem of the nature of the mosaic virus as one which may stimulate to renewed efforts investigation in an almost unworked field, that of the lower orders of life, which it would seem must exist in many other habitats or conditions somewhere.

Sooner or later we must more frequently ask what, if any, are the various connecting links between complex organic compounds and the simplest known living organisms. Surely it is not possible to conceive of bacteria or protozoa as the kinds of living things that would emerge directly from a colloidal nitrogenous matrix. The elaborate correlations existing in the cell as we now know it are stupendous, and it would seem that there must be some simpler life somewhere. The soil and water areas alike should offer the opportunities needed.

Possibly we can know nothing of these because of the difficult technique involved but surely we should not neglect to explore any paths that may lead to fields fruitful in newer facts concerning life. With material at hand so interesting as virus diseases of plants, pathologists and physiologists have an opportunity and a responsibility such as is seldom afforded. Pasteur, as we all know, is commonly supposed to have disproved the idea of the spontaneous generation of life. As students of living beings and of their development, however, we know that he disproved no such thing, but rather he proved that known forms of life did not originate in a brief space of time in a sterilized nutrient fluid. This fact is of incalculable value and has prevented many false theories. Nevertheless, the proof which he offered would not operate to deter investigation that may take us nearer to an understanding of lower orders of life whether or not that may be synonymous with a higher order of chemical substances.

ON SCOLECOSOMES, AND ON SIMILAR BODIES
IN MOSAIC-DISEASED PLANTS[1]

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In 1897 I described in Berichte der Deutschen Botanischen Gesellschaft (15: 577) a remarkable disease of *Anenone nemorosa*. It is characterized by a deformation of the leaves, which sometimes is so strong that the plants may hardly be recognized. Flowers generally are suppressed, and when they are formed they are also altered and not fertile. Therefore, the disease cannot be inherited. Microscopic investigation showed that the number of vascular bundles in the stalks and the number of cells had increased, while their shape had simplified. This is one of the characteristics of kataplasmatic galls. But it was impossible to detect any fungus or animal, which might be the cause, and therefore this deformation may be one of the so-called virus diseases. I have now given it the name of "Alloiophyllie."

In 1908 I began experimental investigation and continued it until the present to answer the question whether the disease might be transferred to healthy plants. Rhizomes of healthy plants were planted in flower pots, and the soil which covered them was mixed with soil in which diseased plants had been growing, or with diseased plants themselves, which had been cut into very small pieces. In this way I got a number of diseased plants every year, and therefore it must be concluded that the alloiophyllie has a living cause, which is able to penetrate into the rhizomes or into the buds from the soil.

Having decided this, I began a new microscopic investigation of stained microtome sections, to find a cause, which perhaps until now had been overlooked. The result was the discovery of very remarkable bodies in the phloem tissues (Figs. 1–5). The cells in which they are present follow each other in long rows in longitudinal direction; but in transverse direction not more than two or three cells containing them were found lying side by side. The number of bodies in each cell is generally large, twenty to forty or even more. In some cases only one, or a few bodies, were found. The shape of the bodies is very various. Most of them are thread-like and straight or a little curved. Sometimes the two halves of a thread are turned around one another in a screw-like manner. In some cases they are spindle-shaped, and others club-shaped, the thin flagellum to which the thinner end is elongated, being straight or turned back to the thick end. The latter type is especially characteristic. In young cells of the buds the bodies are very small, 3–10μ long and only 0.2μ thick. They resemble thread-

like bacteria. In older parts they are longer, 18–30μ long, 0.5μ thick, and the spindle or club-shaped bodies are up to 2.5μ thick, seldom more. Threads split up more or less into two parts are rather frequent. It seems possible, therefore, that they multiply by longitudinal division. The contents of the cells which

Figs. 1–4. Scolecosomes in phloem cells of *Anemone nemorosa:* 1, very thin and small, ×666; 2, spindle- or club-shaped, ×680; 3, thread-like and curved, ×933; 4, single bodies, ×546.

Fig. 5. Scolecosomes of *Anemone nemorosa*, showing variations in shape. ×1400.

contain them is not changed in a visible manner, the nucleus lying in the middle of the cell, surrounded by the bodies at both sides.

The principal place of their occurrence is the vascular bundles of the rhizomes. In several cases they were found in the buds not yet grown out to leaves. I have never seen them in the leaves themselves. They are *not* present in all of the

phloem-strands of the rhizomes, and sometimes they are so scarce that it is very difficult to detect them. It is necessary to investigate longitudinal sections.

From the changing shape and the various curvatures of the threads, they have the appearance of movable organisms. They resemble *Leptomonas* or similar Flagellata, but they are not protozoa because it has not been possible to stain a nucleus. They stain in a homogeneous manner like bacteria, but they can not be bacteria on account of their shape and the manner of dividing. If they are organisms, they must be organisms of a new kind. On account of the worm-like appearance I have proposed to call them "scolecosomes."

The preceding facts have been published (Planta, 1: 419. 1926).[2]

Continuing my infection experiments last year, I succeeded in producing the disease in two other species of *Anemone*, in *A. ranunculoides* and *A. trifolia*. On investigating the rhizomes of the infected plants, scolecosomes were found in great quantity. I tried in vain to infect *Anemone silvestris* and some Ranunculaceae.

While I was still engaged in these studies, I received through the kindness of the author, the paper of Ray Nelson on protozoa-like bodies in mosaic-diseased plants. These bodies are rather different from the scolecosomes, but notwithstanding this, there is a certain similarity. This induced me to investigate some mosaic and virus diseases in the same way, and I will now say some words on the results obtained.

In *Abutilon Thompsoni*, in young internodes not longer than $\frac{1}{2}$ centimeter, I found remarkable bodies similar to a corkscrew, but acute at both ends, in the young sieve-tubes. They are very small, only 12 to 22μ long, and very thin sections, not thicker than 5μ, are necessary to get a good view of them. They are rather scarce and do not occur everywhere; but if one has once detected one of them, in most cases some others may be found in the neighboring parts. Generally there is only one in a cell, lying between the end of it and the nucleus. Sometimes there are two, at the two ends of the cell, having the nucleus between them, or an adult one and some very thin screw-like threads, which appear to be young stages. It seems to be of importance that, stained by the same method, they take a color different from that taken by the scolecosomes of *Anemone*. They do not become red but rather yellowish brown. The nucleus occupies the middle of the cells and seems to be unchanged, only a little less deeply stained than the nuclei of the neighboring cells (Plate I, fig. 1).

Similar bodies were found in potatoes diseased with mosaic, which Professor H. M. Quanjer of Wageningen was kind enough to send me. In "crinkle-mosaic" they were much larger and thicker than those of *Abutilon*, $20-23\mu$, sometimes up to 27μ long, but besides this, of quite the same appearance, and distributed in the same manner in the cells of the phloem tissue, lying in the protoplasm between the nucleus and the cross wall on one or on both sides of the cells (Plate I, fig. 2).

In "intercostal-mosaic" and in "aucuba-mosaic" bodies of the same kind were present, but they were simpler in shape, oval or spindle-like, and with a

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[2] A short abstract appeared in the Berichte d. Deutsch. Botan. Gesellsch. 43: (32). 1925.

EXPLANATION OF PLATE

Intracellular bodies in mosaic-diseased plants.

Fig. 1. Abutilon Thompsoni, phloem cells. ×1840.

2. Potato, variety Bravo, crinkle mosaic. ×1840.

3. Potato, variety Bravo, intercostal mosaic. ×1840.

4. Potato, variety Bravo, mosaic, isolated bundles. ×1840.

5. Potato, variety Bravo, mosaic, phloem cells. ×1060.

6. Tobacco, small oval bodies in phloem cells. ×1220.

7. Tobacco, isolated bundles. ×1840.

8. Tobacco, threads in mesophyll (it is only by accident that the nuclei are cut away in the cells with threads. ×570.

9. Tobacco, threads in epidermal cell (to the right) and in cell below it (to the left).   ×1060.

[In reproduction all drawings were reduced by 3/8 of the original width.]
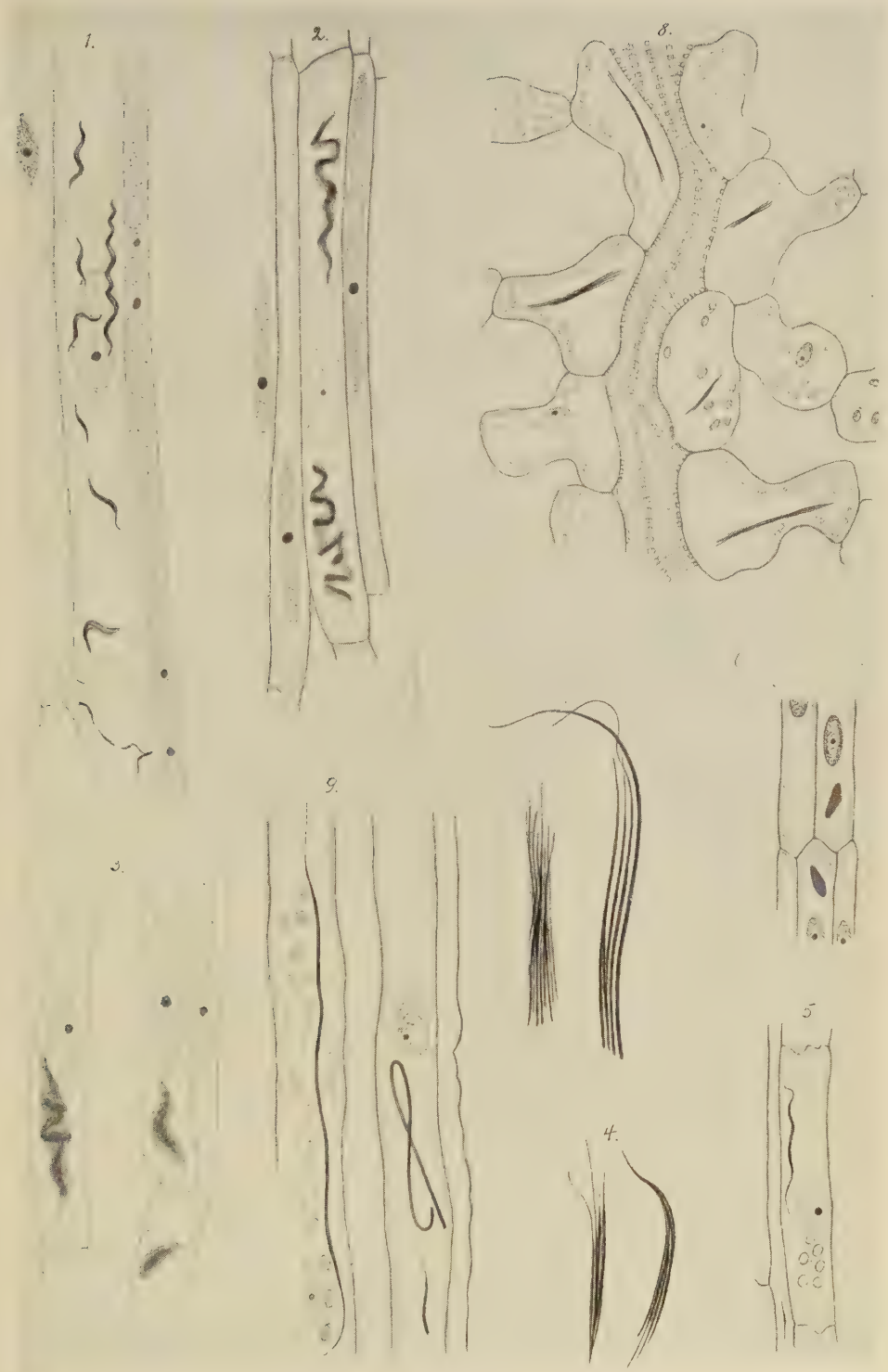
Klebahn: Scolecosomes and Similar Bodies

small trace of screw-structure only, or without it. The investigation is not yet finished, and perhaps more highly developed structures may be found by continued research (Plate I, fig. 3).

A further investigation was made on fixed material of mosaic diseased tobacco plants, which had been sent to the Botanical Garden of Hamburg by Professor Quanjer, some years ago. I first looked for bodies in the phloem-tissue, and indeed in the veins of the very young leaves bodies similar to those described just before in intercostal mosaic were found. But they are small, not larger than the nucleus, and of a simple oval or spindle-like shape (Plate I, fig. 6) Continuing the investigation with more developed leaves I found bodies of quite another kind. They are thin and long threads, sometimes up to 125μ long, in rare cases simple, generally joined together in bundles which are more or less split up at the ends, and the threads a little twisted around each other in a spiral manner (Plate I, fig. 7). They are straight or more or less curved following the shape of the cells which they occupy. Only one thread or one bundle is present in the cells in almost all cases. Small threads or bundles which seem to be young stages were found in the mesophyll of young leaves just developing from the buds. They were found in all tissues with the exception of the xylem only, that is to say, in the phloem, in the mesophyll (Plate I, fig. 8), in the cells below the epidermis (Plate I, fig. 9), in the epidermis itself (Plate I, fig. 9), and even in the cells of the stomata. But they are not present everywhere, and where they are present, cells without them and cells containing them are mixed one with another.

These thread-like bodies of tobacco stain in quite the same manner as do the scolecosomes of *Anemone*, and it may be supposed that they are beings of the same kind and with the same function.

Very similar things were found in a fourth sort of potato mosaic, called merely "mosaic," by Professor Quanjer. They are spindle-like bodies which are split up into or are composed of thin threads (Plate I, fig. 4). They are present in the phloem tissues, but are rather scarce (Plate I, fig. 5). In other material of the same origin, similar bodies were found in some cells of the epidermis and of the parenchyma. Besides these, bodies similar to the cork-screw forms of "crinkle-mosaic" (Plate I, fig. 2) were sometimes met within the phloem.

Concluding these communications, it will be necessary to enter into a short discussion of the facts stated. It is, without doubt, a matter of interest, that in a number of virus diseases bodies have been detected which are not yet known as regular constituents of the cells. Many investigations of various kinds will be necessary to make out the nature and the life history of these remarkable new beings.

As to the scolecosomes of *Anemone*, in my paper in Planta I tried to establish the opinion that they are the cause of the deformation called Alloiophyllie. I could not believe that they were secretions of some substance in the cells. If they are movable organisms, it will be understood that they may penetrate into the soil from diseased plant parts, and from the soil into healthy plants. Here they may produce a virus or an enzyme, which spreads through the sieve tubes to all parts of the plant and causes the deformations in the developing buds. I

cannot prove as yet that they are the cause of the disease, because I cannot say that they are never present in healthy plants. Sometimes they are very scarce even in diseased plants, and the degree of the disease may be so different that a weak infection cannot be distinguished from the healthy condition.

In the manner of staining the thread like bodies of tobacco are very similar to those in *Anemone*, and I am inclined to take them for another kind of scolecosomes. The same holds true for the spindle and thread-like bodies in Quanjer's "mosaic" of potato. But when reviewing the literature, it seemed to me that the bodies detected by Molisch, Mikosch, Amadei, and others in the cells of certain Cactaceae, Orchids, Balsaminaceae, and some other plants and stated to be of albuminoid nature might be the same things. For want of time I could not however, compare them. New questions arise: Are they the same bodies as those in tobacco? If they are, are they regular constituents of the cells, or perhaps were the plants investigated by Molisch, Mikosch and Amadei attacked by some mosaic-like disease? The latter is not quite impossible, because mosaic diseases are perhaps more common than has been known.

The bodies in *Abutilon* and in "crinkle mosaic" of potatoes seem to be very similar to those detected by Ray Nelson, and possibly they are the same things. Certainly they are quite different in kind, from the bodies of *Anemone* and tobacco, although they are similar to a certain degree. The Nelson bodies are said to be found in healthy plants also. Notwithstanding this they may be the cause. For weakly infected plants, perhaps cannot be distinguished from healthy ones, as occurs in *Anemone*, where sometimes only a part of a leaf is attacked. If they are the cause, microscopic investigation must complete the research. Different forms of mosaic may be produced by different organisms, and if two different ones have penetrated into the same plant, complicated forms of diseases may arise. In this connection we must remember "mosaic" of Quanjer, where spindle-shaped and corkscrew-shaped bodies have been found. It is not possible at this moment to give a satisfying answer to any of these difficult questions. New and extended research is necessary to decide them.[3]

[3] The preceding was the contents of my communication before the Congress. In the meanwhile, even before my final manuscript was submitted, I have found scolecosomes also in healthy Anemones. These seemingly movable beings, giving the impression of foreign bodies in the plant, are they really only secretions of the phloem cells? And what may be the mysterious cause of the disease, which may be transferred to healthy plants from infected soil, and through it from diseased plants? I cannot discuss these questions here, but I hope to come back to them in a future paper.

THE ASTER YELLOWS DISEASE[1]

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During the past three years we have given considerable time to studies on the yellows disease of aster. A detailed account of this work will be published in the near future. I now wish to outline briefly some of the results of these studies, to consider them in relation to hypotheses concerning the etiology of virus diseases and to indicate their possible bearing on problems presented by the virus diseases of other plants.

Aster yellows is an infectious chlorosis and a serious disease in the U. S. on the China aster, *Callistephus chinensis* Nees. The aster plant is grown extensively in other parts of the world, especially in Europe and the Orient but yellows is known to be prevalent only in North America. The disease has been widespread and destructive during the past twenty-five years. Whether the incidence of aster yellows has changed during this time is not known. At present it is prevalent throughout the United States. It also occurs in Canada.

A study of the symptoms of aster yellows show that it is somewhat similar to leaf-roll of potato, curly-top of sugar beet and peach yellows. Diseased aster leaves never show mottling. It is, therefore, not a mosaic disease. The first symptom to be observed on a young plant is a slight yellowing along the veins in the whole or in a part of a single young leaf. This symptom, which we will refer to as clearing of the veins, has not been observed in connection with any other aster disease and makes diagnosis possible long before conspicuous chlorosis appears. After a plant has been diseased for some time the new leaves that develop are chlorotic throughout. One half or more, or a sector amounting to less than one half of a plant, may be chlorotic for some time before the remaining portion is affected. Such sectorial infections are characteristic of aster yellows. While chlorosis does not appear in leaves that are mature when the plant is attacked, leaves that are from one half to two thirds full grown and are a normal green color do become diseased, as is shown by clearing of veins and general chlorosis. The disease is systemic in the above ground portions of the plant. It causes chlorosis in all green tissues. Strangely enough, however, petals which normally contain no chlorophyll become quite green when diseased.

Another striking symptom of aster yellows results from the abnormal production of secondary shoots. Instead of lateral buds remaining dormant they produce long thin chlorotic branches.

Plants that contract the disease before they are mature are always more or

[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 18, 1926.

1249

less stunted. The degree of stunting varies with the age of the plant at the time it becomes infected and with the size of the sector infected. The effect of the disease on the main stem is to shorten greatly the internodes. It usually has the opposite effect on the secondary branches. Diseased flowers and seeds are often much larger than healthy ones, but cases also occur where they are dwarfed. The flower heads are always more or less dwarfed. Individual flowers in some cases develop into vegetative branches which may or may not bear small flower heads. Trichomes on diseased flowers frequently develop into leaf-like structures. The petals of ray flowers are uniformly dwarfed. Roots of diseased plants appear to be normal but are on the whole somewhat smaller than the roots of healthy plants.

One of the most interesting symptoms of aster yellows results from the change which it brings about in the response of plants to gravity. Instead of diseased leaves lying flat and making a broad angle with the perpendicular they stand up. A similar response is shown by individual flowers and branches of diseased plants. This modification of the response of plants to gravity is similar to that caused by certain rust and smut diseases where mycelia are systemic.

In brief, it may be said that aster yellows is an infectious disease causing diffuse and well marked chlorosis, clearing of veins, occasional one-sided or sectorial infection, upright habit of growth, malformation and increased growth in certain organs but dwarfing of other organs and dwarfing of the plant as a whole, and the abnormal production of secondary shoots.

We have experimentally transmitted aster yellows to more than fifty different species in twenty-three different families of plants. It has been taken to species in the following families. Compositae, Dipsaceae, Plantaginaceae, Martyniaceae, Gesneriaceae, Scrophulariaceae, Solanaceae, Labiatae, Boraginaceae, Hydrophyllaceae, Polemoniaceae, Asclepiadaceae, Primulaceae, Umbelliferae, Begoniaceae, Resedaceae, Cruciferae, Papaveraceae, Portulacaceae, Caryophyllaceae, Amaranthaceae, Chenopodiaceae, and Polygonaceae.

The disease can no doubt be transmitted to many species of plants that have not been included in our experiments. There are, however, many immune species. I have been unable to transmit it to any plant in the Rosaceae or the Gramineae. Most of the plants to which it has been taken are cultivated flowering plants. It has not yet been transmitted to any plant of great economic importance. I wish to mention, however, that aster yellows is identical with a rather serious disease of lettuce known in the west as the Rio Grande disease and here in New York State as white heart disease.

It is interesting to note that none of the symptoms above mentioned are shown by all species to which yellows has been transmitted. In some plants it does not cause the production of secondary shoots, clearing of veins, or upright habit of growth. In a few cases it causes little or no chlorosis. There might be some doubt as to whether the disease was actually carried to species that do not show the symptoms of yellows as it appears on aster if it were not for the fact that it was transmitted from these plants back to aster and that the disease so transmitted showed all of the symptoms of yellows on aster. The identity of

diseases somewhat similar to aster yellows can not be determined by observation of symptoms.

One of the most interesting and attractive phases of the story of aster yellows is the relation of the disease to its insect carrier. So specific is this relationship that we have come to regard the leaf-hopper *Cicadula sexnotata* Fall. as the insect host of the virus. The aster is a suitable host plant for a number of different insects including the tarnished plant bug, *Lygus pratensis* L., the aphid, *Myzus persicae* Sulz., and the leafhoppers, *Empoasca flavescens* Fab., *Agallia sanguinolenta* Prov., *Graphocephala coccinea* Forst. and *Cicadula sexnotata* Fall. Although these are all sucking insects that feed on the sap of the plants only the last mentioned, *Cicadula sexnotata*, is able to transmit the disease. That the transmission of yellows by this leafhopper is not a simple mechanical transfer is indicated by the persistence of the virus in the insect and by the existence of a long and definite period between the time virus-free insects feed on yellowed plants and the time when they are first able to transmit the disease. We shall refer to this interval as the incubation period of the virus in its insect host. Several methods have been found by which virus-free colonies of *Cicadula* may be gotten and maintained. As long as such colonies are not allowed to feed on yellowed pants they are unable to produce yellows or any injury that shows the remotest resemblance to this disease. If, however, a vigorous colony of virus-free insects are allowed to feed for one day or longer on a yellowed plant the virus is picked up by the insects. But such colonies are unable to transmit the disease until after a period of at least ten days has elapsed. They then transmit it to every plant on which they are allowed to feed. The virus is picked up with apparently equal readiness by each of the five instars of nymphs and by adults. The incubation period varies somewhat with different colonies of insects and with different individual insects. It is generally shorter for adults than for nymphs. It varies from ten days to as much as three weeks but the usual length of the period under ordinary greenhouse conditions, with colonies kept at temperatures of 70°F to 75°F is twelve to fourteen days. It happens that the time necessary for newly hatched nymphs to become adult is approximately equal to the length of the incubation period of the virus in the insect. For this reason nymphs are, under ordinary conditions, unable to transmit the disease. In one experiment, however, where nymphs were reared at low temperatures and their development was slow, the incubation period was completed before they became adult and the disease was transmitted. When nymphs are reared at high temperatures many become adult several days before the incubation period is completed.

The fact that an incubation period is necessary before insects that obtain the virus become inoculative is believed to be important evidence in support of certain hypotheses as to the nature of virus diseases. We have given what might be considered an undue amount of time to a study of this period. Thirty-four experiments were performed which show the existence and approximate length of the incubation period in insects of different ages and with virus obtained from different host plants.

The results obtained with different insect colonies are in close agreement, although some variation is found in the length of the incubation period in different colonies. All experiments show that virus-free insects are unable to transmit yellows immediately after feeding on yellowed plants. It is interesting to note that the minimum incubation period of the virus in the insect is of approximately the same length as the minimum incubation period of the virus in aster plants. The incubation period of the virus in different aster plants varies between rather wide limits. The average for the plants used in our experiments is about 18 days. The period is seldom shorter than 12 days or longer than 24 days. The longest periods shown were by two plants in two different experiments. These showed incubation periods of 38 and 39 days respectively. These periods are considerable longer than those shown by any other plants, and are more than twice the average incubation period. It is interesting that the disease was transmitted to both of these plants by insects in which the virus was just finishing its incubation period. This suggests that the changes which may occur during the incubation period of the virus in the insects may not bave been completed when it was transmitted to the plants but that they had progressed sufficiently to make possible a slow development of the disease. That the condition of the virus in the insect can influence the length of the incubation period of the disease in the plant suggests the occurrence of developmental changes in the virus during its incubation period in the insect.

It has been shown that certain plants on which *Cicadula sexnotata* flourishes are immune to aster yellows. One of these is the rye plant. It was found that virus-bearing colonies cultured on such immune plants retain the virus over a long period of time. Newly hatched nymphs after being allowed to feed on yellowed aster plants were confined on rye plants for two months. During this period they passed through the five instars, became adult and reached old age. While on rye they grew to more than 20 times their original size by weight. When this colony was finally transferred to healthy aster plants it promptly transmitted yellows. This and other similar experiments prove that when once picked up the virus is retained by at least some of the insects as long as they live, even when cultured on immune plants. This retention of the virus over long periods indicates that it is not loosely held in the body of the insect.

It was found that not all individual leafhoppers obtain the virus when allowed to feed for one day or longer on yellowed aster plants. This suggested that certain individuals might not take it up and might be incapable of becoming carriers of the disease. Thirty leafhoppers hatched and reared to maturity on a yellowed aster plant were caged individually on a series of healthy plants. A colony of thirty similar individuals were caged on another series of plants. All of the leafhoppers that lived carried the virus. Individuals incapable of carrying the disease were not present among those selected for the test. One of the most interesting points brought out by this experiment is the apparent loss of the virus by certain individuals that were for some time inoculative. It is also interesting that considerable variation is shown by different individuals in their ability to inoculate plants.

I do not wish to take time to discuss in detail our failure to transmit aster yellows mechanically by means of juice or crushed tissues from diseased plants, by means of feces from virus-carrying insects, etc. The disease was transmitted by budding. It is not transmitted through the eggs of virus-carrying insects or through the seeds of diseased plants. It lives over winter in biennial and perennial host plants. Aster yellows is similar to but distinct from peach yellows and the curly-top disease of beets. It is not identical with the stunt disease of Dahlias.

In summarizing, it may be said that aster yellows is an infectious chlorosis prevalent in the United States and Canada but not known in other parts of the world. It is transmitted by a leafhopper which was probably imported into this country fifty or more years ago. This insect is common in Europe and the Orient where the aster and other host plants of the disease are widely grown. Aster yellows, however, is not known to occur in European or Oriental countries. The virus of this disease has apparently not yet reached them.

Although aster yellows attacks a wide range of host plants it is very specific in its insect relationships. That the disease is not transmitted by its insect carrier in a simple mechanical way is indicated by the existence of a long and definite incubation period of the virus in its insect host, by the retention of the virus by insects over a long period of time, even when they are cultured on plants immune to the disease, by the long incubation period of the disease in plants exposed to insects in which the virus is just finishing its incubation period and by our failure to transmit it mechanically except by budding.

It is believed that the intimate and specific relationship which has been shown to exist between the aster yellows disease and its insect carrier brings important evidence that the causative agent is biological rather than chemical, for it is difficult to concieve of any agent other than a living organism that would require an incubation period in its insect carrier or would be retained by this insect over long periods of time in the absence of susceptible host plants.

Our work suggests that a better understanding of virus diseases of plants, both from the practical and the scientific view-point will result from further studies on their insect relationships. They are probably all insect borne diseases. Some of them may cause diseases of their insect carriers as well as of their host plants.

UEBER PANASCHIERUNG[1]

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Wenn wir von Panaschierung sprechen, muss stets eine Verständigung über den Sinn vorausgeschickt werden, in welchem jenes Wort gebraucht werden soll.

Unter dem Sammelbegriff Panaschierung werden ausserordentlich mannigfaltige Erscheinungen zusammengefasst, deren gemeinschaftliche Züge sich darauf beschränken, dass durch den Wechsel blasser und grüner Anteile in den Blättern irgendwelcher Pflanzen eine irgendwie gestaltete Zeichnung oder "Buntblättrigkeit" zustande kommt. Die Entwicklungsgeschichte dieser Sprenkel und Flecken, ihre Histologie, ihre Aetiologie, ja sogar ihr Einfluss auf die äussere Erscheinung der vorliegenden Pflanzen können ausserordentlich verschieden sein. Nähere Prüfung dieser Mannigfaltigkeiten lassen keinen Zweifel daran, dass das mit Panaschierung sich beschäftigende Kapitel der Pflanzenpathologie Dinge in sich schliesst, die nur in unwesentlichen Merkmalen mehr oder minder gut miteinander übereinstimmen, in anderen Zügen aber so grundsätzlich von einander abweichen, dass im Interesse einer sicheren Verständigung es zu beklagen ist, wenn der Terminus der Panaschierung herkömmlicher Weise auf so heterogene Dinge angewandt wird; viele Unklarheiten, welche sich beim Studium der älteren und auch der neuen Literatur fühlbar machen, sind darin begründet, dass sich so oft bei den Angaben der Autoren nicht feststellen lässt, auf was für eine Art der Panaschierung sie sich beziehen.

Es hat sich als zweckmässig erwiesen, zwei Gruppen von Panaschierungen zu unterscheiden,[2] und es darf als eine Erleichterung für die wissenschaftliche Beschäftigung mit der Panaschierung bezeichnet werden, dass die Zugehörigkeit einer buntblättrigen Pflanze zu der einen oder anderen Gruppe bereits bei makroskopischer Prüfung ermittelt werden kann. Wir unterscheiden: 1. Panaschierungen, bei welchen blasse und grüne Anteile mit unscharfen Grenzen aneinander stossen, so dass ein derart gezeichnetes Blatt aus grünen und blassen Zellen, in den Randzonen aber auch aus halbgrünen und schwachgrünen aller Schattierungen sich aufbaut,—und 2. Panaschierungen, bei welchen blasse und grüne Anteile mit scharfen Grenzen sich berühren, deren Schärfe auch mikroskopischer Prüfung standhält, derart, dass normal grüne und blasse Zellen unvermittelt aneinander stossen, und das panaschierte Blatt nur aus zwei Zellensorten —völlig grünen und extrem blassen—sich zusammensetzt.

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[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 18, 1926.

[2] Küster, Pathologische Pflanzenanatomie, 3 Aufl. (p. 18). 1925.

Zu der ersten Gruppe gehören vor allem die als Fleckenpanaschierungen bezeichneten Erscheinungen, sowohl die den *Aucuba*-Typus repräsentierenden, wie die den Leitungsbahnen der Blätter folgende Zeichnungsart oder wie die "infektiöse Chlorose" von *Abutilon* und anderen Malvengewächsen und die grosse Schar der Mosaikkrankheiten. Die zur zweiten Gruppe gehörenden Panaschierungen, die namentlich von sehr zahlreichen Sorten unserer Ziergehölze bekannt sind (*Evonymus, Weigelia, Cornus, Acer, Elaeagnus* usw.), auch an krautigen Zierpflanzen wie namentlich an *Pelargonium*-arten in unseren Gärten uns allenthalben begegnen, weisen je nach dem Verteilungsmodus der blassen und weissen Areale sehr verschiedenen Habitus auf: erscheinen die Blätter zur Hälfte grün, zur Hälfte blass oder sektorenartig in zahlreiche keilförmige Stücke verschiedener Farbe aufgeteilt, so liegt sektoriale Panaschierung vor; erscheint die bunte Spreite in kleine oder grössere, unregelmässig geformte und durcheinander gewürfelte Stücke zerlegt, so spricht man von marmorierter Panaschierung; sind die einzelnen grünen und blassen Anteile sehr klein, so dass die Blätter ein fein gesprenkeltes Aussehen annehmen, so handelt es sich um pulverulente Panaschierung; wenn wir schliesslich grüne Blätter mit breitem oder schmalem weissem Rand ausgestattet sehen, so haben wir es mit weissrandiger (albimarginater) Panaschierung zu tun; seltener als diese ist der umgekehrte Fall, dass die Blätter einen tief grünen Rand haben, der ein mattgrünes Binnenfeld umfasst (viridimarginate Panaschierung). Nur auf die wichtigsten Unterschiede in der Verteilung der grünen und blassen Felder konnte hier hingewiesen werden.

Die Untersuchung der panaschierten Pflanzen ist in den letzten Jahrzehnten von vielen Forschern in Angriff genommen und in den verschiedensten Richtungen gefördert worden. In der Tat stellen die panaschierten Pflanzen mit ihren Zellen und Gewebestrukturen, ihrer Physiologie und Aetiologie viele Fragen an den Forscher, deren Beantwortung nicht nür Klärung sehr eigenartiger pflanzenpathologischer Fragen, sonderen auch im weiteren Horizont der allgemeinen Physiologie und Biologie wichtige Aufschlüsse zu bringen verspricht. Auf einige Fragen, welche die Untersuchungen der letzten Jahre behandelt, zum Teil auch schon ihrer Beantwortung näher gebracht haben, soll im folgenden eingegangen werden.

Zytologie. Die Zellen der blassen Anteile panaschierter Blätter enthalten Chromatophoren, welche frühzeitig verblassen oder trotz Belichtung usw. nicht zum normalen Ergrünen kommen.[3] Besonders einflussreich für die Entwickelung panaschierter Blätter ist das Licht: an hellen Standorten ist der Farbunterschied zwischen grünen und blassen Anteilen stark betont, an schattigen Standorten ist der Farben- und Helligkeitsunterschied zwischen diesen und jenen geringer—eine alte Erfahrung, die sich die für kontrastreiche Farbentönung des Laubes interessierten Gärtner und Züchter längst nutzbar zu machen verstehen. Bei besonders weitgehender Reduktion des Chlorophylls sind in den farblosen Zellen schliesslich nur noch gelblichgrüne oder gelbe oder sogar farblose Chromatophoren nachweisbar. Während man noch vor kurzem der Meinung

[3] Vgl. Schürhoff, P. Die Plastiden. Linsbauer, Handbuch der Pflanzenanatomie 1: 1924.

tung grosse Mannigfaltigkeiten indem bald kleine, bald grossee Arale verschiedener Farbe mit einander wechseln, und ihre räumlichen Beziehungen zu Blattrand und Blattrippen usw. den verschiedensten Gesetzen zu gehorchen haben —sondern auch in der vertikalen (d.h. der zur Blattoberfläche senkrecht stehenden): bei sektorialen und marginaten Panaschierungen lässt der Blattquerschnitt meist deutlich eine treppenförmig abgestufte, nur selten eine glatt abschneidende Grenze zwischen blassen und grünen Arealen erkennen; zwei, drei oder mehr Stufen greifen in wechselnder Verzahnung ineinander, derart, dass zuweilen die grünen Mesophyllplatten sich nur um wenige Zellenbreiten einander überragen, in anderen Fällen (vgl. Fig. 1) die einen sich ansehnlich weit über die anderen
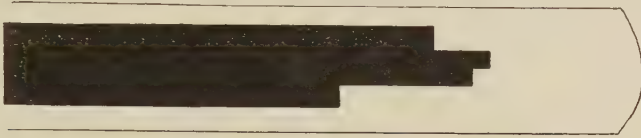
Fig. 1. Treppenförmig abgestufte Grenze zwischen grünen und blassem mesophyll.

vorschieben. Selbst an den verschiedenen Stellen des nämlichen Blattes zeigen die grünen und blassen Anteile oftmals auffallend stark wechselnde Profilierungen. Von grösstem Interesse sind die von marmorierten und pulverulenten Panaschierungen gelieferten Querschnittsbilder; die grünen Gewebeanteile bilden auf ihnen keine zusammenhängenden Massen mehr, sondern zeigen sich in Form kleiner oder grosser grüner Sprenkel, die bald eine, bald zwei oder mehr Zell-
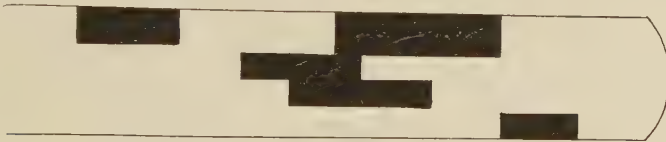
Fig. 2. Verteilung der grünen Gewebeanteile auf dem Querschnitt eines marmorierten Blattes.

schichten mächtig sein und in regelmässiger Verteilung bald in dieser, bald in jener Höhenlage im Mesophyll liegen können (Fig. 2).

Die beschreibende und vergleichende Histologie der panaschierten Pflanzen hat mit einer Fülle auffallender Verteilungsbilder bekannt gemacht. Auf Fragen von allgemeinem Interesse stossen wir dann, wenn wir die physiologischen Beziehungen der grünen und blassen Anteile zu einander prüfen. Makroskopisch bei vielen bunten Pflanzen leicht zu bestätigen ist es, dass die weissen Anteile der Blätter im Flächenwachstum stark hinter den grünen zurückbleiben, so dass oft die unregelmässigsten Verbiegungen und Verbeulungen der Spreite die Folge sind. Bei anderen panaschierten Arten sehen wir freilich keinen nennenswerten Wachstumsunterschied zwischen den grünen und blassen Anteilen; die farblosen Spreiten erreichen dieselbe Grösse wie die grünen, die $\frac{1}{2}:\frac{1}{2}$ sektorial geteilten Spreiten behalten die Symmetrie normaler Blätter usw. Bei mikroskopischer Untersuchung stellt sich heraus, dass auch das Dickenwachstum, und dass die

Höhe der einzelnen Mesophyllschichten in panaschierten Blättern mancher Arten sehr verschieden sein kann; bei Blättern, deren Struktur der in Fig. 2 dargestellten entspricht, kann die ungleiche Dicke, welche bestimmte Gewebeschichten in ihren grünen und blassen Abschnitten erreichen, zu einer auffallenden Deformation der einzelnen Schichten führen. Es mag nahe liegen, die Hypoplasie der blassen Anteile auf den Ausfall der Assimilationstätigkeit zurückzuführen und die hierdurch bedingte schlechte Ernährung der Zellen, welche für die blassen Anteile sich voraussetzen liesse; mit dieser Annahme ist die Beobachtung, dass selbst bei Arten einer Gattung oder Spielarten einer Spezies eine Entwicklungshemmung der blassen Anteile bald sehr sinnfällig wahrzunehmen ist, bald völlig ausbleibt, schlecht zu vereinigen, so dass zu prüfen wäre, ob nicht irgend welche Stoffwechselprodukte der blassen Zellen es sind, welche ihr Wachstum in vielen Fällen aufhalten.

Künftige Untersuchungen werden ferner zu prüfen haben, welcher Art die Korrelationen sind, die zwischen den Mesophyllschichten eines Blattes bestehen, und welche Wandlungen sie in panaschierten Blättern erfahren. Bei manchen panaschierten Arten ist höchst auffallend, dass auch ihre grünen Mesophyllzellen sich in ihren Blättern anders verhalten können, als in normal gebauten, dass sie zu erstaunlicher Länge heranwachsen, dass sie am Rande der grünem Gewebeplatten eine andere Ausbildung erfahren können als in deren Mitte, dass sie zwischen die farblosen Zellen sich gleichsam einzukeilen und jene zu verdrängen imstande sind.[6] Es fehlt nicht an Fällen, in welchen von den blassen Gewebelagen nur zusammengedrückte schmächtige Zellenreste übrig bleiben.

Ontogenese. Wir fragen uns weiterhin, auf welchen entwicklungsgeschichtlichen Wegen die auffällige Zusammensetzung der Blätter zustande kommt. Eine Antwort scheinen die marmorierten und pulverulenten Panaschierungsformen nahe zu legen. Bei ihnen und ganz ebenso bei den in Blüten und auf Laubblättern vieler hybrider Gartenformen—am schönsten wohl bei den zahllosen Varietäten des *Coleus hybridus* gefundenen Anthozyansprenkelungen[7]—drängt sich uns der Gedanke auf, dass die zu irgendwie geformten Gruppen vereinigten grünen und blassen Zellen Abkömmlinge einer Zelle sind, und dass in vielen Kombinationen benachbarte Gruppen aus Deszendenten zweier Geschwisterzellen sich aufbauen, die verschiedene Anlagen in sich enthielten und daher verschieden ausgestattete Nachkommenschaft aus sich hervorgehen liessen; die hypothetische Zellenteilung,—durch welche ungleich veranlagte Geschwisterzellen entstanden sind, nennen wir eine inäquale Teilung. Unmittelbarer Beobachtung zugänglich sind bereits eine Reihe von inäqualen Teilungen gewesen, bei denen leicht sichtbare Zellenteile, wie die Chromatophoren, ja selbst die Tochterkerne sich inäqual auf die Tochterzellen verteilen. Dass bei der Enstehung panaschierter Organe ungleichartige Verteilung geformter Zellenbestandteile eine Rolle spielen könnte, ist nicht erwiesen, liegt aber nicht ausserhalb des Bereiches der Möglichkeit. Vielleicht sind aber auch inäquale Teilungen und inäquale

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[6] Hierüber und über verwandte Erscheinungen vgl. Küster, E. Anatomie der panaschierten Blätter. Linsbauers Handbuch der Pflanzen-Anatomie, 1926.

[7] Küster, E. Die Verteilung des Anthozyans bei Coleus-Spielarten. Flora **110**: (p. 1). **1917**.

Ausstattung der Tochterzellen unabhängig vom Schicksal der geformten Zellen-einschlüsse vorstellbar.[8]

Die Hypothese, Differenzierungen wie die der marmorierten oder pulveru-lenten Blätter auf inäquale Teilungen zurückzuführen, nimmt nicht an, dass zwei Geschwisterzellen durch ihre Entwicklungsmöglichkeiten sich unterschei-den, sondern dass jene in ihrem Reaktionsvermögen gegenüber irgendwelchen von der Aussenwelt oder ihrer belebten Nachbarschaft ausgehenden Einflüssen irgendwie sich unterscheiden. Dieselbe Theorie würde zu erklären imstande sein, dass die Sprenkelungen mancher panaschierter Blätter in ihrer Grösse so ver-schieden sind, dass sie zuweilen ansehnlichen Umfang gewinnen, in anderen Fällen zur mikroskopischen Kleinheit herabsinken; die Theorie würde solche Unterschiede mit dem Zeitpunkt erklären, zu welchem die inäqualen Teilungen stattfinden: je später die sich vollziehen d.h. je weniger Teilungen zwischen ihnen und dem Abschluss der Teilungstätigkeit noch liegen, um so kleiner wer-den die von den Abkömmlingen der inäqualen Geschwister gebildeten Grup-pen ausfallen müssen; ist die letzte Teilung eine inäquale, so leiten sich von ihr nur eine grüne und eine blasse Zelle ab.

Wir haben bisher nur auf marmorierte und pulverulente Panaschierungen Bezug genommen; in der Tat scheinen bei diesen die Verhältnisse leichter zu überblicken zu sein, als bei sektorialen und marginaten. Wenn wir grüne und blasse Sektoren in gleichbleibender Breite auf ansehnliche Entfernungen hin einen Spross färben sehen, oder wenn eine albitunikate Pflanze in allen ihren Teilen mit einem blassen Gewebemantel ausgestattet ist, so liegt die Vorstellung nahe, dass schon im Vegetationspunkt eine Sonderung der Zellen beiderlei Art eingetreten ist. Baur hat eine solche Annahme bereits vor Jahren formuliert. Dass sie viele Erscheinungen gut zu erklären vermag, ist kein Zweifel, und daher ist ihr Erfolg gut begründet; namentlich lassen sich mit ihr auch die den Gärtnern schon seit langer Zeit bekannten Erscheinungen der Wurzeltriebbildung erklä-ren, auf welche neuerdings durch Bateson die Aufmerksamkeit wieder gelenkt worden ist;[9] Triebe, die sich aus den Wurzeln randpanaschierter Pelargonien entwickeln, also aus dem Gewebekern der Pflanze herleiten,[10] oder welche nach Verwundung als Anventivtriebe aus bunten Sprossen entstehen,[11] sind nur ausnahmsweise bunt, im allgemeinen rein grün. Es darf anderseits nicht über-sehen werden, dass gar manche Erscheinungen schlecht mit Baur's Theorie zu vereinigen sind, namentlich wenn man gleichzeitig mit ihr auch die Lehre an-nehmen will, dass aus rein weissen Zellen stets nur ebensolche Deszendenten sich herleiten, und ihnen niemals eine Rückkehr zur Produktion von grünen

[8] Küster, E. Ueber Mosaikpanaschierung und vergleichbare Erscheinungen. Ber. d. Deut. Bot. Gesellsch. 36: (p. 54), 1918. Küster, E. Patholog. Pflanzenanatomie 3. Aufl. p. 407ff), 1925. Noack, K. L. Entwicklungsmechanische Studien an panaschierten Pelargonien, zugleich ein Bei-trag zur Theorie der Periklinalchimären. Jahrb. f. wiss. Bot. 61: (p. 459). 1922.

[9] Bateson. Root-cutting, chimaeras and sports. Journ. Genetics 6: (p. 91). 1926; Bateson. Root-cutting and chimaeras. Ibid. 11: (p. 91). 1921; Bateson. Somatic segregation in plants. Versl. Internat. Tuinbouw-Congr., Amsterdam (p. 155). 1923.

[10] Magnus, P. Botan. Zeitg. 30: (p. 249) 1872; dort Hinweis auf Lemoine.

[11] Küster, E. Regenerationserscheinungen an Bakteriengallen. Flora 120: (p. 170). 1926.

Zellen möglich ist. Zu solchen Erscheinungen rechne ich die auf dem blassen Rande mancher weissrandig panaschierter Blätter beobachtete Entwicklung grüner Sprenkel,[12] ferner die Inversion der Panaschierung d.h. die Umkehrung der Zeichnung, durch welche aus weissrandigen Individuen unvermittelt oder allmählich grünrandige Sprosse hervorgehen, bei welchen ein grüner Gewebemantel um einen blassen Kern gelegt erscheint, oder durch welche selbst an einer Blattspreite grünrandige und weissrandige Abschnitte sich kombinieren.[13] Andere Wege der Erklärung werden durch Noack gewiesen, der (a. a. o.) die Entscheidung über das Schicksal der Zellen auch für die marginaten Panaschierungen auf einem relativ späten Stadium der Entwicklung sucht. Auch bei diesem Versuch, die Ontogenese der marginat-panaschierten Sprosse und Blätter zu erklären, handelt es sich freilich zunächst noch um eine unerwiesene Annahme.

Aetiologie: *Einfluss äusserer Bedingungen.* Gleich bedeutungsvoll für die Zwecke des Züchters und Liebhabers einerseits, für Fragestellungen der allgemeinen Physiologie und Pathologie andrerseits wäre es, panaschierte Pflanzen willkürlich aus normalen grünen entstehen lassen zu können. In der Tat sehen wir panaschierte Individuen wie Mutationen unter den Aussaaten plötzlich erscheinen, ja sogar bunte Aeste aus grünen Exemplaren wie durch Knospenmutation hervorgehen, schliesslich auch an einzelnen Blättern grüner Pflanzen hie und da eine Sprenkelung sich zeigen (Beobachtungen an *Dahlia, Taraxacum,* u. a. m.). Solche Erfahrungen legen die Annahme nahe, dass irgendwelche Aussenweltbedingungen die besagten Anomalien zu veranlassen im stande sind. Es hat nicht an Versuchen gefehlt, durch Variation der Ernährung, der Wasserversorgung, der Belichtung, der Temperatur, durch Anwendung von Giften usw. Panaschierungen hervorzurufen. Die Ergebnisse sind negativ geblieben; wohl lässt sich eine vorhandene Panaschierung weitgehend beeinflussen, fördern oder zum Verschwinden bringen—doch ist bisher kein Weg gefunden worden, sie willkürlich zu erzeugen. Immerhin liegen einige Beobachtungen vor, welche die Hoffnung der Forscher auf eine Beantwortung jener Frage noch stützen können: de Vries[14] teilt mit, dass bei *Eupatorium cannabinum* über den von *Pterophorus microdactylus,* einer Fadenmotte, erzeugten Gallen sehr oft die Blätter der Wirtspflanze starke Panaschierung aufweisen; allerdings hält de Vries für wahrscheinlich, dass der Gallenreiz lediglich eine in den Wirten latente Anlage zur Panaschierung manifest gemacht habe. Weiterhin darf ich auf die noch der Prüfung und Bestätigung bedürftigen Untersuchungen von Kissling[15] und Stein[16] verweisen: Kissling erzielte nach Injektion schwacher Kaliumnitratlösungen in die Fruchtknoten seiner Gerstenpflanzen panaschierte Nachkommen;

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[12] Küster, E. Ueber weissrandige Blätter und andere Formen der Buntblättrigkeit. Biolog. Zentralbl. **39**: (p. 212). 1919.

[13] Küster, E. Anatomie der panaschierten Blätter, 1926 (Linsbauer's Handbuch der Pflanzenanatomie).

[14] de Vries, H. Mutationstheorie **1**: (p. 291). 1901; **2**: (p. 490, 491). 1903.

[15] Kissling, L. Einige besondere Fälle von Chlorophylldefekten Gersten. Zeitschr. f. indukt. Abstammungs-u. Vererbungslehre **19**: (p. 160). 1918.

[16] Stein, E. Ueber den Einfluss von Radiumbestrahlung auf Antirrhinum. Zeitschr. f. indukt. Abstammungs-u. Vererbungslehre **29**: (p. 1). 1922.

Stein liess Radiumstrahlen auf Samen von *Antirrhinum* wirken und beobachtete an den jungen Pflanzen neben mancherlei anderen Anomalien auch sektoriale Streifung der Blätter, von der sich nach der Verfasserin Angaben nicht mit Bestimmtheit sagen lässt, ob sie den hier behandelten Panaschierungen wesensgleich oder wenigstens wesensähnlich waren. Alle diese Versuche sind bei weitem nicht ausreichend, um die Frage nach der experimentellen Erzeugbarkeit der Panaschierungen zu beantworten; sie sind aber als Anregung und Ermutigung zu neuen Studien zu begrüssen.

Dass Aussenweltsfaktoren die Farbenkontraste, den Reichtum der Zeichnung usw. weitgehend beeinflussen können, dass sogar unter bestimmten Bedingungen bunte Pflanzen ihre Zeichnung verlieren, unter anderen wiedergewinnen, liesse sich an vielen Beispielen erläutern. Mit der erforderlichen Exaktheit sind aber bisher nur vereinzelte panaschierte Pflanzen auf die Abhängigkeit ihrer Buntheit von äusseren Bedingungen geprüft worden.[17] Es kann nicht zweifelhaft sein, dass verschiedene Gewebeformen der Pflanzenorgane das Optimum ihrer Entwicklung keineswegs unter denselben Bedingungen erreichen. Auch für die blassen und normal grünen Gewebeanteile bunter Blätter ist ein solcher Unterschied vorauszusetzen. Heinricher[18] hat durch experimentelle Arbeit auf die unterschiedlichen Ansprüche der beiden Gewebekomponenten hingewiesen. Bunte Exemplare von *Tradescantia fluminensis* verlieren bei Kultur im Schatten allmählich ihre Panaschierung,—nicht dadurch, dass die blassen Anteile ergrünen, sondern in der Weise, dass sie von einem Internodium zum anderen immer schmaler werden und schliesslich ganz verschwinden und ausgemerzt werden. Der Befund scheint zu beweisen, dass Bedingungen, welche dem grünen Gewebe oder den normal veranlagten Gewebeanteilen der Sprossspitze noch eine normale Entwicklung gestatten, den anderen eine solche bereits unmöglich machen.

Aetiologie: innere Bedingungen. Wenn von inneren Bedingungen die Rede sein soll, welche auf die Panaschierung Einfluss haben, so kann es sich nur um diejenigen handeln, welche das von den "Korrelationen" handelnde Kapitel der Entwicklungsmechanik so inhaltsreich und vielseitig machen. Auf korrelative Wirkungen führen wir viele Unterschiede zurück, die in Grösse und Struktur der Erstlings- und der Folgeblätter einer jungen Pflanze, zwischen basalen und apikalen Anteilen eines Jahrestriebes usw. bestehen. Solche Unterschiede begegnen auch bei Beurteilung der Panaschierungsbilder ausserordentlich oft. In vielen Fällen sehen wir gesetzmässig auf rein grüne oder mit grünen Arealen reichlich ausgestattete Blätter solche folgen, bei welchen die blassen Anteile immer reichlicher ausfallen (progressive Panaschierung)—oder sehen wir im Verlaufe der Sprossentwicklung die blassen Anteile mehr und mehr zurücktreten (regressive Panaschierung). Auf die Wirkung innerer Bedingungen werden wir auch in denjenigen Fällen schliessen dürfen, in welchen sich Beziehungen zwischen dem

[17] Küster, E. Zur Aetiologie der Panaschierungen. Zeitschr. f. Pflanzenkrankheiten **36**: (p. 129) 1926.

[18] Heinricher, E. Rückgang der Panaschierung und ihr völliges Erlöschen als Folge verminderten Lichtgenusses; Beobachtungen und Versuchen mit Tradescantia fluminensis Vell, var. albo-striata. Flora **109**: (p. 40). 1917.

Panaschierungsbild und der typischen Asymmetrie der Blätter erkennen lassen (*Aspidistra, Ulmus*),[19] in welchen Basis und Spitze der Spreiten, Blattrand und Binnenteile mit Panaschierungssprenkeln verschieden, aber in gesetzmässig wiederkehrender Weise ausgestattet werden, oder in welchen das Zurückschneiden bunter Gehölze zum Austreiben schlafender Knospen und auf diesem Wege zur Produktion abweichender Panaschierungsbilder oder blasser Albinotriebe führt.

Phänologie. Auch phaenologische Beobachtungen veranlassen uns, irgendwelche Störungen der Korrelationen für das Verhalten panaschierter Pflanzen und Sprosse verantwortlich zu machen. Hinsichtlich des Beginns der Winterruhe verhalten sich grüne, bunte und weisse Aeste des *Acer negundo* deutlich verschieden: zuerst kommen die grünen zur Ruhe, später die scheckigen; die Albinotriebe bleiben am längsten tätig und schliessen vielfach ihre Knospen gar nicht, so dass ihre Spitzen schliesslich im Herbst zu Grunde gehen.[20] Weisse Triebe können auch im Herbst im Gewächshaus leicht zum Treiben gebracht werden. Die Frage nach den Ursachen der phänologischen Anomalien ist noch nicht endgültig geklärt.

Vererbungslehre. Seitdem Baur, Correns, Stomps und andere durch zahlreiche Versuchsreihen die Vererbung der Panaschierungsmerkmale geprüft haben, ist deutlich geworden, welche Fülle von Unterschieden auch unabhängig von äusserer Erscheinung und histologischer Struktur im Bereich der Buntblättrigen vorliegen und der Analyse bedürfen. Hinsichtlich der Vererbbarkeit der Buntheit nach Mendel's Regeln, der Unabhängigkeit der Nachkommenschaft von den Qualitäten und der Herkunft des Pollenkorns und des Verhaltens bei Selbstbestäubung bestehen tiefgreifende Unterschiede. Seit Correns können wir von einem panaschierten "Status" in denjenigen Fällen sprechen, in welchen zwar das Auftreten farbloser Zellen, nicht aber das Panaschierungsbild genotypisch festgelegt ist, von einer buntblättrigen "forma" besonderer Art dann, wenn auch das Panaschierungsbild erblich fixiert ist. Von einer Klassifikation der Panaschierungen nach den von der Vererbungsforschung gefundenen Gesichtspunkten sind wir freilich noch weit entfernt. Dass die fortgesetzten Bemühungen um eine solche namentlich auch wichtige Beiträge zur allgemeinen Physiologie und Pathologie der Zelle bringen werden, lassen vor allem die Untersuchungen Correns' hoffen.[21]

[19] Küster, E. Anatomie der panaschierten Blätter, 1926 (Linsbauer's Handbuch der Pflanzenanatomie).

[20] Lakon, G. Ueber die jährliche Periodizität panaschierter Holzgewächse. Ber. d. Deut. Bot. Gesellsch. 34: (p. 639). 1916; Lakon, G. Ueber die Festigkeit der Ruhe panaschierter Holzgewächse. Ibid. 35: (p. 648). 1917.

[21] Zusammenstellung der wichtigsten Literatur bei Schürhoff a. a. O.

SOME REMARKS ON THE PHYSIOLOGICAL
ASPECTS OF PARASITISM[1]

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At the present time the importance of adding to our knowledge concerning the physiological relationships which exist between parasite and host is becoming fully realized by workers interested in questions of plant disease. To be sure, soon after the parasitic relation was clearly defined in plants, some notable contributions were made by DeBary and others, while the work of Ward and coworkers upon *Botrytis* and the rusts, and of Jones on soft rot bacteria will always stand as pioneer studies in this field. For the past decade such studies as those of Blackman, Brown and coworkers in England, Allen, Stakman, Harter, and others in America, have done much to clear up old doubts and add new facts which make for a clearer understanding of the fundamental relations which underlie this important phase of plant pathology.

I shall not attempt at this time even to outline the status of our present knowledge. Time would hardly permit it and furthermore it would be superfluous following the comprehensive résumé which has only recently been furnished by Blackman ('24). His paper brings before us clearly the wide diversity of situations extending from the simpler types, of which that of *Botrytis cinerea* Pers. is an example, to the complex relationships which prevail in the rusts and mildews. These various types must be studied from the most promising angle. It is my purpose to discuss a few specific cases.

I wish to consider first some results which have been secured with certain of the storage rots of onion. *Colletotrichum circinans* (Berk.) Vog., which causes the onion smudge disease, is confined pretty largely in its parasitic phase to the onion bulb. It may, under suitable conditions, cause the death of young seedlings, but after the plant is well started the fungus has little or no power to attack, except as it may occasionally subsist upon senescent leaf tissue and the dead leaf bases which are sloughed off continuously. As the plant matures then, the organism is normally present only as a saprophyte but as such it readily establishes itself in the dry dead outer skins of the bulb, except in colored bulbs, as will be discussed later. Once the plant becomes dormant the succulent scales of the bulb are subjected to attack. Yellowish sunken lesions appear which enlarge only slowly but persistently. The disease is not ordinarily very serious economically, and the parasite is only mildly aggressive. The case is one of the simplest in so far as parasitism is concerned.

[1] Presented before the International Congress of Plant Science, Section of Pathology, Ithaca, ew York, August 19, 1926.

The mode of penetration is that of direct entry through the cuticle, which becomes necessary, of course, since there are practically no stomata on the bulb scales. The mechanics of penetration is essentially the same as that described by Dey ('19) for *Colletotrichum lindemuthianum* (Sac. and Mag.) Bri. and Cav. The infection hypha having penetrated the thin external layer of cutin differs from that of the latter species in that instead of penetrating the subcuticular wall at once, it proceeds to develop just beneath the cuticle, stretching and raising the latter perceptibly. Just why this delay is occasioned is not understood. The ability of the fungus to dissolve its way through the cell wall is later demonstrated. The gelatinization of the cell wall takes place more rapidly if the inoculated bulb is kept continuously in the moist chamber, which demonstrates no lack of cytolytic properties; and the question arises as to whether the host cell itself exerts a retarding influence upon the hyphae before they penetrate the subcuticular wall.

At this point we may consider the effects of the extracted cell contents upon the fungus (Walker'23, Walker, Lindegren, and Bachmann'25). It was noted that the spores of the fungus were killed in onion scale extract and that only in dilutions of one part to one hundred or more did germination take place. The toxins were shown to consist in part of the volatile substances which arise from onion tissues, especially when crushed. A single drop of extracted juice placed in an ordinary Petri dish was often sufficient to preclude germination of spores in the same chamber. The volatile toxins, while not completely killing the mycelium, would in the same concentration decidedly check growth. Heating the juice at 70°C. for 15 minutes or more drove off or destroyed the volatile toxins, but after exposure at 96°C. for one and one-half hours a residual, non-volatile toxin still remained in the juice. It is, of course, possible that the toxicity in the latter case may have been due to substances formed during the heating process.

We are at once led to question to what degree these toxins in the cell sap influence the invading hypha. It is one of the strange coincidences of plant life that this organism should have become adapted to a parasitic relation upon so adverse a substrate. Were we able to follow with certainty the chemical and physical changes which go on in the cell more light might be thrown upon the interrelations between the host and parasite, but our present methods do not always afford an easy solution. As soon as penetration of the cuticle occurs, there is an evident change in the protoplast of the underlying cell. There is quite likely sufficient action in advance of the fungus to start degeneration of the protoplasm, but this is much slower than in the case of *Botrytis cinerea*, for instance, where the solution of the middle lamella takes place quite speedily once infection is established. The effect is brought out more strikingly when red bulbs are used. In this case the anthocyan is present in the cell sap of the outer epidermal cell. When infection drops are placed upon the succulent scales penetration of the cuticle takes place as promptly as in the white bulb. By stripping off the epidermis under such drops and observing *in toto* it is easy to see that the infection hypha has barely become established beneath the cuticle when disintegration of the anthocyan in the underlying cell lumen sets in. The reduction of color is

probably only coincident with other pathological effects upon the protoplast.

Though it has not been possible to learn what other chemical changes are going on, it may not be out of place to speculate for the moment. May we not conceive of a situation wherein a struggle between parasite and host is taking place? How far can the volatile toxins influence the hypha without the wall, thus retarding the fungus? How soon does the degeneration set up within the cell by the infection hypha result in breaking down the volatile toxin? Eventually the hypha enters the cell lumen and thus the fungus gradually makes headway. But, on the other hand, there remains the possibility that the host through its cell constituents holds back the fungus and reduces it to a weak, inaggressive parasite. It seems quite plausible that the toxicity of the cell sap explains the fact that *C. circinans* is seldom observed as a wound parasite. We are accustomed to look upon wound parasites as among the weakest invaders. In this case it appears that invasion through wounds is excluded, but invasion by the more complex method of cuticular penetration provides the parasite with certain advantages whereby it seemingly sufficiently overcomes the host toxins to make slow progress.

With the collapse of the epidermal cell, the underlying parenchyma cell shows similar pathological effects, and the process thus continues. One can not be certain whether the degeneration of the first host cell may have some detrimental effect on the adjacent cells, though this seems quite possible. As supporting this possibility may be cited a common observation in the red onion scale. Normally, the anthocyan is found only in the epidermal cells. If now infection is produced on the inner scales of the bulb where the development of anthocyan is not yet completed, it is not uncommon to observe the production of anthocyan in a zone several cells deep in the parenchyma around the young lesion. These cells appear to be perfectly normal except for the production of pigment and it is quite evident that the effects of invasion are being felt for some little distance around the lesion quite a while before any pathological changes are apparent.

Another case of interest in this parasitic relation is that which concerns the resistance to invasion of colored bulbs (Walker '23, Walker and Lindegren'24). The reactions so far described, with the exception of the pigment production in the parenchyma of red bulbs, are the same for white and colored varieties. Under natural conditions the latter remains quite free from attack while white bulbs in general are susceptible. The evidence shows that another toxin distinct from that already discussed as present in the cell of succulent scales is found only in the resistant varieties. This substance is readily extracted in cold water from the dry outer scales. Its close association with the production of pigment indicates that it may indeed be one or another of the pigment compounds. As the infection drop comes in contact with the outer dead scales, the diffusion of the toxin results and thus spore germination or growth of the fungus is held in abeyance. This procedure seems to afford an effective barrier against attack.

The living, succulent scales being ordinarily surrounded by this dead colored sheath are effectively protected. The vulnerability of the living tissues is revealed

if they are exposed to inoculum by chance splitting of the outer scales or by artificial removal. One can not be certain that the "pigment toxin" as such is present in the outer epidermis of the living scale but we might well expect it to be present or in the process of formation, for the pigment, red or yellow, is already in evidence. In any case, were it present, the nature of the cell precludes its diffusion through the cellulose and cutin walls into the infection drop. The fungus may germinate, therefore, penetrate the cuticle, and establish itself just below the cutin without coming into contact with the pigment. At this point, as already described, the pigment disappears in the epidermal cell and the fungus appears to be impeded no more than in the white bulb. The disintegration of the pigment may well be the natural result of the disintegration of the protoplast, but in that case it is one of the earliest signs of pathological effect. If it is the direct effect of fungus secretion then the organism is in a better position than before to exert such an effect. In the dead outer tissue, by way of contrast, the rapid and unimpeded diffusion of the "pigment toxin" into the infection drop throws the balance in the opposite direction.

The neck rot fungus, *Botrytis byssoidea* Walker, is now mentioned by way of comparison because it offers a quite distinct type of parasitism upon the same tissue (Walker '26ᵃ, Walker and Lindegren '24). Initial infection through the cuticle is uncommon. The reason for this is not understood. It does take place where a greater mass of mycelium is present than would ordinarily occur on the outer scale. Thus, when one scale becomes affected and the mycelial mat next to the underlying scale develops, penetration of the latter takes place commonly and readily. Infection usually occurs through senescent tissue at the neck of the bulb or through wounds, principally through such as are made upon the cutting of tops. The extracted juice though markedly toxic to the organism is not as decidedly inhibitive as in the case of *C. circinans*. Thus a few spores may germinate in the diluted juice and growth proceeds slowly. There is evidence that infection through wounds is often much delayed and perhaps excluded by the action of the toxin in the living host cell. Successful infection depends upon the fungus being able to establish itself to the point where its secretions may break down the tissue in advance. Thereupon it develops rapidly upon the by-products of host cell decomposition. Its secretions are then much more potent than in the case of *C. circinans*. Thus although the initial establishment of the parasite is much more uncertain and apparently repelled somewhat more effectively in the beginning than the smudge organism, the decay is much more rapid once the balance is shifted in favor of the parasite. As evidence of how readily this balance is upset is the fact that sudden desiccation of the tissues being broken down in advance, by the enzymes of *B. byssoidea*, checks further advance of the parasite. The mycelium may thus remain in the desiccated tissue alive but entirely impotent for an indefinite period. The control of neck rot through rapid desiccation of the neck tissues of the bulb has been based upon knowledge of this fact (Walker '25).

The diversity of conditions which prevail between even closely related cases of parasitism is exemplified when we compare the observations just noted for

onion smudge with those which obtain in the case of bean anthracnose, caused by the sister species, *Colletotrichum lindemuthianum*, as described by Leach ('23). Here penetration takes place in a similar manner, but if the host is susceptible no evidence of detrimental effect upon the protoplast of the host cell is seen in the beginning. The fungus passes through the wall in a very small opening while the remainder of the membrane shows no effect. Passing into the cell lumen the mycelium appears to enlarge without visible effect upon the protoplast and even to pass on to adjoining cells with no more effect upon the walls and protoplasm. Thus in this early stage the parasite appears to maintain a relation suggestive of the higher type so common with the obligate parasites. Quite suddenly, however, there is a complete shift in the balance and the parasite then advances rapidly causing softening of the cell walls and rapid disintegration of cell contents. In the resistant host the mycelium penetrates the epidermal cell and possibly one or two surrounding cells, but there is no early harmonious relation. From the beginning the cell walls react differently, and prompt disintegration of the protoplast occurs while the hyphae are incapable of further development.

Let us now turn from the more fundamental phase as revealed by the study of cellular pathology in the strictest sense to a consideration of some of the grosser aspects. The study in recent years of the relation of environment to the development of disease has opened some interesting questions which deal with the changes exerted upon parasitic relations. In the study of the temperature effects upon disease an analysis of the relation to the parasite and to the host independently reveals that very often the response of one varies from the response of the other while development of disease may vary from either.

In a study of cabbage yellows, Tisdale ('23) found the organism to produce the most rapid growth on potato agar at 25°-27°C. The growth of the host was best at soil temperatures around 20°C. The optimum for the disease was 26° to 29°C. and this followed closely the reaction of the fungus. In tobacco root rot— *Thielavia basicola* (B. and Br.) Zopf—Johnson and Hartman ('19) found the optimum for the growth of the fungus on agar at 25°C. or above. The optimum for the host development was 20 to 25°, while the greatest development of the disease was 17° to 18°C. In the case of white rot of onion (*Sclerotium cepivorum* Berk.) the optimum for growth of the organism on potato agar is between 20° and 25°, the greatest root and top growth of the host at 20° to 22°, while the disease is most aggressive at 15° to 18° (Walker '25). Other cases might be cited.

There is, of course, a certain danger in laying too much emphasis on the response of the organism on culture media. The substrate is at best quite removed in constitution from the host tissue and we are aware that optima may vary even with the same organism on different artificial substrates. The rate of extension of mycelium, which is the criterion commonly used as the basis of comparison, may be among the least important factors in pathogenesis. Enzyme production and secretion of toxins or of staling products may well have distinct optima, and these factors are admittedly quite as important as vegetative extension. On the other hand, they are less easily evaluated. Much the same may be said of the host. Growth as measured by dry weight is the first logical method

of analysis. But it is more important eventually to consider the more subtle end-products of metabolism as revealed by tissue analysis, approached by micro-chemical and macrochemical methods.

Realizing the importance of the last consideration, Dickson ('25) approached the question with these points in mind. He has made an intensive study of the seedling blights of wheat and corn caused by *Gibberella saubinetii* (Mont.) Sacc. In this instance the same parasite attacks two hosts which grow best at widely different temperatures. Wheat does best in a cool soil, while the corn is a relatively warm temperature plant. This gave an opportunity to determine whether the influence of temperature upon parasitism was exerted through effects upon the fungus or upon the host as well.

The optimum for growth of the organism on potato dextrose agar was 24° to 28°C. The hardiest wheat plants were produced at soil temperatures from 8° to 12°C. Corn seedlings developed best at soil temperatures from 24° to 28°C. The seedling blight of wheat does not occur below 10° but increases rapidly as the temperature rises above that point. In corn, on the contrary, the disease is greatest at 8°, and is severe up to 20°, but is completely checked at 24°.

A study of the differences in host metabolism and composition at various temperatures reveals some significant facts. The wheat seedlings grown at low temperatures are high in soluble carbohydrates such as dextrin, sucrose, and hexoses, while the cell walls are well lignified in the cortex of the coleorhiza and coleoptile which are the main regions attacked. The high temperature wheat plants are low in these carbohydrate building substances and high in pentosans. The (low temperature) plants, which evade the organism most successfully, therefore have cell walls which are most capable of resisting fungus invasion, while the hexoses and polysaccharides most common in these plants were shown to be relatively poor sources of carbon for the parasite. The high temperature wheat plants present an opposite condition. The cell walls are poorly reinforced against the mycelium while pentosan-yielding substances which were predominant were found to be excellent food for the fungus. In the corn the reciprocal condition prevails. The low temperature plants (most susceptible) are most like the high temperature wheat plants, that is, the pentosan-yielding substances are high and they predominate in the cell wall in the protective sheath tissues. The high temperature corn plants (most resistant) have a large reserve of hexoses and polysaccharides, while the cell walls of the protective sheath tissues are of cellulose impregnated with suberin.

This is a case where environment, particularly temperature, in so far as the studies go, has a profound effect upon parasitism through its influence upon host metabolism and in the end upon the composition of the cell membranes and the production of carbohydrate reserves which serve as food for the parasite. Already these findings have been extended to a consideration of differences between various selfed lines of corn wherein the variation in expression of resistance seems to be based in large measure upon the type of host metabolism (Dickson and Holbert '26).

A still more recent contribution by Conant ('26) deserves mention in this

discussion. This has to do with the reaction of tobacco to invasion by *Thielavia basicola*. As stated before this organism grows fastest on culture media at 25°C. or above, but is most pathogenic at 17° to 18°, while the optimum for root development of the host is 20° to 25°. Conant has made a critical histological study wherein he compared first a series of varieties which represented gradations from very susceptible to very resistant at the optimum temperature for the disease. Secondly, he compared the reactions of a susceptible variety at 20°C. where the disease is quite severe, at 25°C. where it is attenuated, and at 30°C. where it is absent.

The fungus is unable to penetrate the suberized epidermal cells of very young roots or the outer layer of cork cells in older roots except by mass action. In over 50 per cent of the cases observed infection occurred in the natural wounds occasioned by the rupturing of the cortex and epidermis by secondary roots. In the susceptible varieties the fungus thus gaining entrance advances rapidly in the cortex and may reach the stele. Main conducting roots are thus readily incapacitated. In an extremely resistant tobacco variety such as Xanthia the proliferation of cork cells around the invading hyphae either in the primary cortex of young roots or in the periderm of older roots is undoubtedly the key to the successful escape from severe damage by the fungus. It is quite clearly shown that the activity of the tissues below the fungus is stimulated to the formation of a phellogen layer. In the susceptible varieties this reaction on the part of the host is so meager and so delayed as to be of little value as a protective agency. Varieties which occupy an intermediate condition between the very susceptible Maryland Broadleaf and the very resistant Xanthia show a corresponding degree to which the activity in the pericycle results in "corking out" of the parasite.

The same type of reaction seemed to be responsible for the increased resistance of susceptible varieties (Burley, for instance) when grown at 25°C. or higher instead of at 20°C. Under this environment phellogen activity was decidedly increased, with the result that strong reactions to the fungus became more common. Whereas the delimitation of the fungus is due directly to the obstruction by cork cells, Conant leaves open the obvious question as to whether the composition of the cortical or periderm cells of the resistant plant may not be influential in restraining the parasite while cork cells are being formed. Regardless of how this latter query may eventually be answered, the fact still remains that we have here a striking case of response of the host to parasitic invasion. Once the root is entered the disturbance is felt for some distance and the immediate effect is the stimulation of the normal function of host cells which fortunately results in a protective barrier. It is also significant that in the plant which is classed as susceptible the fundamental discrepancy is that of delay in pericyclic activity, while under a suitable environment this is speeded up sufficiently to become effective.

The ever-growing importance of a better understanding of the basis of differences in susceptibility and resistance among varieties of a given species probably does more than any one thing to stimulate our interest in questions relating to parasitism. The diseases discussed serve to illustrate the intricacies involved.

Certain toxic substances contained in the living cells of the onion which might be expected to serve as an effective barrier against the parasite are common to both resistant and susceptible varieties, while the actual expression of resistance is concerned with a substance functional only in the dead outer colored scales. In the case of tobacco root-rot the defense on the part of the host comes subsequent to infection and it is apparently stimulated through invasion by the parasite. And of more than passing interest is the suggestion from the works cited on seedling blight of corn and root-rot of tobacco that the inherited differences between resistant and susceptible varieties or strains seem to have, in these two instances, the same fundamental basis as the variation induced by changes in environment. But let us be cautious in generalizing, and rather seek more facts.

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NUCLEAR PHENOMENA IN PUCCINIA
TRITICINA PHYSIOLOGIC FORM XI[1]

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In the course of a series of cytological studies of cereal rusts, undertaken for the purpose of learning more about the interaction of host and parasite in different types and gradations of susceptibility and resistance, a number of irregularities in nuclear behavior were noted. They occur in the leaf rust of wheat, *Puccinia triticina* physiologic race XI.

The leaf rust of wheat was formerly included with other species under the name of *Puccinia rubigo-vera*. Eriksson separated it under the name *Puccinia triticina*.

The uredinia and telia are found on wheat. Until recently, the aecial host was unknown, in spite of numerous attempts to determine it. The work of Jackson and Mains in 1921 proved that the aecia are borne on species of *Thalictrum* native to Europe and Asia, particularly *T. delavayi* and *T. flavum*. In America, where the rust has been introduced and where the aecial host is practically absent, the rust probably lives on as a continuous series of uredinial generations.

Infection by urediniospores takes place through the stomata which in wheat are abundant on both surfaces of the leaf. The germ tube from the spore grows along the leaf surface to a stoma. Then the protoplasm along the whole length of this tube flows on into the tip, forming there an aggregation called the ap pressorium. When unobstructed it rounds up into a hemispherical cushion of rather dense protoplasm just over the end of the stomatal aperture. A septum isolates it from the germ tube. Two or more appressoria may occupy the same stoma, crowding and more or less deforming each other. Fully formed appressoria have four nuclei or sometimes more.

Entrance is usually effected near the end of the stoma. The delicate wall of the appressorium collapses as its contents pass through the stomatal slit to form the vesicle within. The substomatal vesicle lies in contact with the inner face of the guard cells. It is a rounded body containing dense cytoplasm and nuclei. When a stoma carries more than one appressorium both may enter. The number of nuclei in the vesicle varies. There may be 4 nuclei or 8, or even more.

Entrance counts were made of fungi fixed in the morning, 40 hours after inoculation. The great majority had entered. Only 37 out of 204 (about 18 per cent) still remained outside.

An abundance of spores was used in this inoculation, and stomata crowded with appressoria are of rather frequent occurrence. Among them are seen masses

[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 19, 1926.

of fungous plasm which in size and conformation suggest a fusion of two appressoria. In some cases the two germ tubes leading into them are still present. In a few cases the two appressoria effect separate entries and then the sub-stomatal vesicles become connected. The volume of the united vesicles is at least twice that of a single one. In all the young material studied containing stages of entry into the host, about 4 per cent showed fusion.

There is evidence that these combined appressoria and combined sub-stomatal vesicles are capable of further development and give rise to mycelium within the host.

After entry in the ordinary procedure the fungous plasm originally present in the spore is massed in a rounded vesicle just inside the stoma, and this move has been accomplished without food other than that originally stored in the spore. The next step is the formation of the infecting hypha. The hypha grows inwards across the air chamber beneath the stoma, taking a course at right angles to the epidermis of the leaf.

Cytoplasm and nuclei flows into this infecting hypha, leaving the vesicle nearly or quite evacuated. On striking a mesophyll cell a septum may form just back of the tip giving rise to a short terminal cell, the haustorium mother cell. Six nuclei remain in the infecting hypha after forming this terminal cell.

The haustorium mother cell gives rise to a small haustorium within which appears a single well-formed nucleus. In no case observed up to the 6th day at least, has the host cell suffered visibly from the invasion. It is not plasmolyzed, collapsed, nor even impoverished. The only disturbance noted is in the host nucleus, which moves over to the haustorium, and may even become wrapped around the young haustorium, partly enclosing it.

In all cases the infecting hypha gives rise to one or more branches soon after its own advance is checked by the formation of a haustorium. These branches grow, come in contact with host cells, form haustorium mother cells and haustoria, and in their turn branch. The repetition of this process soon forms a rich branching system of hyphae. Early in this development, the older hyphae are seen to be partly or completely empty, their contents apparently having drained towards the growing tips. This probably does not mean that nuclei and cytoplasm as such, flow on to the tips, passing through the intervening septa. The protoplasm is probably broken down, perhaps by some autolytic process and translocated in some simpler, more soluble form. This conservation of materials speeds the advance of the fungus.

As already noted, the spore has 2 nuclei, the appressorium 4 or more, the substomatal vesicle commonly 8, and the infecting hypha after forming the first haustorium mother cell, often contains 6. In the further development, one or two of these nuclei are usually left behind close to the substomatal vesicle, the others divide and their progeny become distributed to the branches. Early hyphae of the young fungus have somewhat irregular nuclear content. Four or even more nuclei in a cell are not rare. Soon, however, groups of 3 nuclei become conspicuous.

Hundreds of these groups of 3 nuclei have been encountered in infections of

different ages, grown at different times of year, and on different hosts. It is not a simple matter, however, to determine that vegetative cells are regularly tri-nucleate. The hyphae are confined to the irregular communicating air spaces of the spongy mespohyll tissue, and it is seldom possible in sectioned material, to trace an individual hypha through any great distance. Moreover, the vege-tative cells are long, the septa delimiting a cell are thin, and in young hyphae with dense cytoplasm, are easily overlooked. When occasionally, cell limits are clear, especially in older partly drained hyphae it is evident that we do deal with trinucleate cells. It is not obvious why the number should be 3 at a stage when other rusts aie binucleate. This trinucleate condition in a myceliun does not originate in connection with a fusion of two appressoria at the beginning of infection. Young mycelia occur with characteristic groups of 3 nuclei, in which it can still be determined with certainty that a single appressorium was present at the point of entry.

Haustoria form and expand freely. They are regularly uninucleate. In view of the multinuclear mycelium giving rise to them, it was of interest to trace their origin and growth. When the tip of a hypha strikes against a host cell and its growth in length is forcibly checked for the moment, the changes preparatory to haustorium formation set in. The nuclei divide, one set of daughter nuclei moves out into the thickened tip of the hypha, and a cross wall formed just back of this tip isolates a short terminal cell, the haustorium mother cell. This cell usually flattens out somewhat against the host cell wall and often becomes shoe-shaped. It has regularly 3 nuclei, rarely 2 or 4. These nuclei become markedly reduced in size.

The contents of the haustorium mother cell now pass through the wall into the host cell. First a slender tube forms extending into the host cell usually at right angles to the wall at that point. The cytoplasm and the 3 minute nuclei of the mother cell pass through this tube or "neck" of the haustorium forming at its inner end a dense globular head within which at first no details of structure can be seen. By absorption of water it soon expands and the cytoplasm of the haustorium opens into a reticulate structure within which appears a single globular nucleus. This nucleus contains a rather coarse chromatin net and a single densely-stained rounded granule at its periphery.

What has become of the other 2 nuclei? None remains behind in the mother cell. Do all 3 fuse to form the single nucleus found in the haustorium, or do 2 of the 3 degenerate? A study of half-grown haustoria shows the regular presence of 2 small dense bodies in the cytoplasm, usually located near the nucleus and on opposite sides of it. Sometimes these appear fragmented. Ordinarily they disappear as the haustorium matures but may occasionally still be seen. It seems probable, then, that the central nucleus of the group survives and the other two nuclei degenerate.

In shape, the great majority of the haustoria are cylindrical or worm-shaped. A few become irregularly branched. They attain large size. The maximum is close to 50 microns.

The nucleus of the host seems to be powerfully attracted by the haustorium.

It is often seen flattened out against the haustorium. A nucleus may be drawn out into a dumb-bell shaped body having contact with two neighboring haustoria, or extended into a lobe almost disconnected with the main body of the nucleus to form contacts with more distant haustoria. It has been commonly believed that haustoria move to the nucleus of the cells they invade. Here, on the contrary, there is little room to question that it is the nucleus that moves to the haustoria. This activity of the nucleus would seem to be independent of the rest of the cell contents—there is no marked flow of host cytoplasm to the haustoria. This contact of nucleus and haustorium does no visible harm to either body in susceptible hosts—both continue to live and function.

At the beginning of reproductive activity there comes a marked change in nuclear relations. Any section through the margin of a uredinium where the spores are still young and thin-walled shows that spores are uniformly binucleate. It is not easy to determine the nuclear content of the cells beneath as they are partly drained. Occasionally, however, cells at some depth below the surface are seen to be binucleate.

Feeding hyphae at the center of the infection are too closely interwoven to make it possible to determine cell limits. Moreover, the translocation of food materials from the central mycelium to the reproductive areas at the surface has left these hyphae nearly empty, and their nuclei, when visible at all, are vague.

It is in the marginal regions of the infection if anywhere, that the mode of origin of the binucleate condition is to be determined. Apparently it is only in cells soon to give rise to spores that this change takes place, for vegetative hyphae of the deeper tissues still show the groups of three nuclei. Even a week or ten days after reproductive activities have begun, one may still see them in feeding hyphae in the outskirts of the infection.

But along the line of spore formation just below the epidermis, short binucleate cells form. As the uredinium spreads radially, more and more of the sub-epidermal mycelium changes character, and this takes place considerably in advance of spore formation. Sub-epidermal binucleate cells may sometimes be found 150μ beyond the young spores. Attempts have been made to discover just how this change takes place. Theoretically it might happen in several ways.

The binuclear condition would be established if one nucleus of a trinucleate cell divided forming a cell with four nuclei and a cross wall separated it into 2 cells of 2 nuclei each. Sub-epidermal cells containing 4 nuclei occur, but if binucleated cells arose in this fashion it would be difficult to prove it after the event for the result of an ordinary division of a binucleate cell would look the same.

A binucleate cell might arise by the degeneration of one of the 3 nuclei, by some process similar to what regularly occurs in the haustorium. In some cases there are indications of this but it is not proved.

Two nuclei of a trinucleate cell might fuse, giving rise to a binucleate cell. No evidence for this can be given. At this stage the cells are short and their nuclei are usually in contact. Occasionally one sees a large nucleus with 2 nucleoles but in itself this cannot count as proof of fusion.

The binucleate condition would also be reached if a trinucleate cell should divide into 2, leaving 1 nucleus behind in the penultimate cell and 2 in the terminal cell. In its further growth the terminal cell would give rise to a series of binucleated cells. This appears to happen in some cases.

Occasionally a cell is seen containing one full-grown nucleus and a pair of half-grown nuclei. This condition probably arose by the independent division of one of the nuclei of a cell which had already become binucleate. Evidently the simultaneous divisions which maintain the binucleate condition in other rusts are not well established in this readjustment period.

Two instances of fusion of hyphae have been seen in sub-epidermal areas where spores are about to form. In both cases, 2 hyphae converged and fused and an enlarged mass formed at the point of union. Coming out of the fused mass are 1 abortive hypha, and 1 vigorous hypha. The fusing hyphae are probably closely related.

How frequently, and under what conditions this type of fusion occurs is not known. Both of these cases were found in the relatively free space of a sub-stomatal cavity. Even here, they would have been overlooked after other hyphae had closed in around them.

Taking place as it does in tissues about to form spores, this fusion is also vaguely suggestive of the fusion at the base of the aecium of other rusts. Nothing is known of the nuclear phenomena here, nor of the later development from it, nor what share, if any, it has in the establishment of the binucleate spore-bearing tissue.

By whatever process or processes the shift to the binucleate condition takes place, it works efficiently. The mother cell of the spore is regularly binucleate and at its division both the spore and the stalk cell receive two nuclei.

Long cycled rusts show a regular sequence of nuclear phenomena and a definite alternation of generations. The uninucleated or gametophytic generation begins with the sporidium, continues through the aecial mycelium, the pycnia, and pycniospores. In a layer of cells at the base of the aecium the transition to the binucleated condition occurs, either by the migration of a nucleus from one cell to another or by the resorption of the walls between 2 adjoining uninucleated cells.

The layer of binucleated or sporophytic cells so initiated gives rise by conjugate divisions to binucleated aeciospores. The binucleate condition or sporophyte is maintained on through the uredinial generations. Only in the young teliospores do the 2 nuclei fuse. On the germination of the teliospore the fusion nucleus divides twice and there is evidence that these are reduction divisions. The sporidia borne on the promycelium start the gametophyte once more.

Numerous deviations from this regular cycle are recorded in the literature of rust cytology, and to these can be added the minor aberrations found in *Puccinia triticina* XI.

Puccinia triticina so far as known has lived on in America for an extended period by means of an unbroken line of uredinial generations. Teliospores form, to be sure, and germinate, but in the absence of the aecial host this is a blind

alley in the life cycle, and the only effective continuance is by means of uredini-ospores.

This long-continued uredinial series takes place without apparent diminution in the vigor of the fungus. Cytological study of this strain of the rust, however, has revealed irregularities which might be variously interpreted as signs of oncoming degeneration or as sporadic ill-defined ways of compensating for the missing sexual part of the cycle. Briefly summarized, these are:- (a) the occasional fusion of 2 appressoria or of 2 sub-stomatal vesicles; (b) regularly multinucleated cells in the first hyphae followed by (c) the conspicuous groups of 3 nuclei and trinucleate cells throughout the vegetative development; (d) regularly uninucleate haustoria from trinucleate haustorium mother cells; (e) occasional fusions of hyphae where spores are soon to be formed; and (f) a complete return to the binucleate condition in the spore-bearing tissue, which then produces normal binucleate spores.

It is doubtful what weight to give to these variations. No comparative study has been made of this rust passing normally through its complete life cycle. This makes difficult an evaluation of the irregularities found here. A comparison of them with the unusual nuclear behavior found elsewhere in the rusts may be of interest.

Multinucleated cells in the first hyphae of the uredinial mycelium of *Puccinia triticina* and several other rusts were observed by Pole-Evans in 1907. He seems to regard them as cases of delayed septation. Ward figures 2 to 4 nuclei in cells of the young uredo mycelium of *P. dispersa*.

Multinucleated cells have been found by several workers at the base of the aecium associated with the process of fusion.

Lindfors finds that the uninucleate mycelium of the primary uredo of *Trachyspora alchemillae* which spreads throughout the host plant may become multinucleate in the cramped quarters of the embryonic tissues of the host, but becomes uninucleate again as those tissues expand. He believes that this should be considered as essentially uninucleate. In *Puccinia glumarum*, the uredo mycelium is multinucleate but becomes binucleate in reproductive areas. In these cases the nuclei are numerous and indefinite in number and throw little light on the groups of three nuclei found in the vegetative growth of *P. triticina* XI.

Trinucleate cells have been figured by a number of students of rust cytology, but are quite uniformly sporadic cases of triple fusion. At the point of transition from the uninucleate to the binucleate condition (at the base of the aecium in the long cycled rusts, and in the primary uredo or the telium in the abbreviated cycles) in a few cases 3 nuclei become associated instead of 2. Spores arising from these trinucleate basal cells are also trinucleate. The fate of these spores is unknown. These, too, are of little aid in explaining the present case as the urediniospores giving rise to the mycelium of *P. triticina* are binucleate.

It may well be that one should extend Lindfors's recommendation to cover this case and consider it equivalent to the binucleate condition because it begins and ends with a binucleate spore. Even so, it remains unexplained why the

number of nuclei here should be predominantly—almost uniformly *three*, through all but the youngest vegetative development.

The production of regularly uninucleate haustoria from trinucleate haustorium mother cells is not far out of line with other rusts but has no exact parallel in the literature so far as noted. Haustoria of different rusts are recorded as having 1 to 5 nuclei, the number is sometimes variable even on the same mycelium, and the number of nuclei in the haustoria is either the same as that of the mycelium bearing them, or less. Haustoria in *P. triticina* XI come within these limits but appear to be more definite and uniform than other rusts.

The significance of the fusion of the fungi at the stoma is not known. Not all of the literature has been covered, but no case like it has been noted.

There is no known provision in the usual life cycle of rusts for bringing together nuclei of different parentage.[2] One might indulge in interesting speculations as to the possible share fusions such as these might have in the production of new physiologic forms of the rust. It should be borne in mind, however, that no pairing of nuclei or nuclear fusions have been proved here.

Even a brief survey of rust cytology suffices to impress one with the plasticity of the nuclear history in rusts with altered and abbreviated life cycles. In this connection it should be borne in mind that even the regular process of fusion at the base of the aecium is commonly believed to be a substitute for an earlier form of reproduction in which the pycniospores functioned as male cells. In rusts without an aecium Christman finds a very similar fusion in the first uredinial generation, and in certain of the micro- and lepto-forms Lindfors finds fusion at the base of the telium. Moreover, the fusion is not necessarily between the cells which give rise directly to spores—it may occur several cell-generations earlier in the vegetative mycelium. Morphological evidence of the plasticity of the rusts is given by Dietel who traces the derivation of reduced types from the corresponding heteroecious or autoecious forms. The teliosori of the reduced species occur in small or large groups like the *aecia* of the corresponding heteroecious type and bring about the same deformation of host tissues.

In an *Endophyllum*, Hoffman finds an aecium of normal appearance producing aeciospores which germinate like teliospores by producing promycelia the sporidia of which lead directly to more aecia. Recent work by Kunkel and Dodge on the orange rusts of *Rubus* show that side by side with the regular long-cycled rust (0, I, III) there occurs a short-cycled form in which the aeciospores germinate by forming promycelia, thus returning directly to the uninucleate condition and eliminating the telium. Moreover, Dodge finds some evidence of a "third or intermediate type which is maturing aecia of two kinds," and which, "may represent a strain of *Gymnoconia* which is particularly unstable and from which a short-cycled rust is now arising and which will have distinct morphological characters of its own."

These few instances show the shifts and makeshifts to which the fungus has been put in the exigencies of parasitic life. They show the plasticity of the rusts in being able to shift the processes of fusion and reduction from one part of the

[2] Since this was written J. H. Craigie has announced heterothallism in rusts.

life cycle to another, and the persistence of the processes themselves under varied conditions and alterations of the life cycle. Isolated instances occur where both fusion and reduction appear to be lost, but these are exceptional.

It would be interesting to know whether the aberrations in nuclear behavior observed in *Puccinia triticina* XI are to be regarded as an expression of the need of, and an ill-defined attempt at compensation for the excised part of the life cycle. Also whether ultimately a revised nuclear history is to be expected, such as has been achieved and is being achieved in other rusts, by means of which *P. triticina* would be rendered independent of any aecial host.

CORRELATION BETWEEN THE HOST ANATOMY AND THE DEGREE OF SUSCEPTIBILITY FOR PHYTOPHTHORA INFESTANS IN POTATO TUBERS[1]

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To all pathologists it is a well known fact that the accurate knowledge of characteristics correlated with the varietal degree of resistance in a host plant is most desirable. As is also well known, unlike what might be expected, such a correlation can but seldom be traced.

Valleau found some correlation between the condition of the lenticels in the skin of plums and the degree of resistance against *Sclerotinia cinerea,*—still the degree of hardness of the flesh of the fruit played its part too. Dr. Pietsch, whose observations were published in condensed form after his death, found by 3300 measurements a correlation between the size of the stomatal openings and the degree of varietal susceptibility of carnations to the attack of *Uromyces caryophyllaceus.*

For potato tubers I investigated the qualities that might be the cause of a varietal degree of susceptibility for *Phytophthora infestans.* It was found that several qualities come into play here.

The first and most important quality that may cause resistance in tubers is only to be investigated when the tubers are unripe; the cork-cambium is active then and thus the skin may be drawn off without causing any injury to the underlying parenchyma. Tubers treated in this way were immersed in a suspension of sporangia in water that was kept during some hours, so that zoospores might reasonably be expected to abound. On treating tubers of many varieties in this way the effect of the inoculation appeared to be widely different. After 3 or 4 days tubers of all varieties showed a lot of small brown spots, each spot marking the place where a germ-tube had managed to enter into the parenchyma. When tubers of different varieties were inoculated, an examination after 8–10 days might show very divergent results; either the spots might have increased and the tuber show the diffuse livid coloration due to an invasion by *P. infestans,* or the spots might not have increased in size and the inner part of the tuber remained quite free from any invasion of the fungus. In such a case the variety examined had a quality of resistance sharply localised in the cork-cambium. When tubers of such a resistant variety were inoculated in a slit of the parenchyma the extension of the fungus was the same as in tubers non-resistant in the cork-cambium. Thus as sharp a localization of a quality of resistance was

found here as had been found by Walker for an attack of *Colletotrichum circinans* in respect to the colored bulbscales of onion. Forty-five varieties tested in this way gave the following results:

Varieties tested	Per cent of inoculated tubers where many spots appeared
17	100
24	93–33
1	14
1	4
2	0

It may be noted that two varieties among those most used in heavy clay soil in Holland (Bravo and Roode Ster) were among those most resistant. Probably this quality has much to do with their popularity. By putting to the test existing seedlings of these two varieties it was ascertained that the quality is inherited.

A genetic investigation was not undertaken. This quality which is one that may be tested reliably under laboratory conditions protects the tubers thoroughly under varying soil conditions.

Obviously the next question is in respect to what kind of quality we meet here. Microscopically no anatomical difference in the phellogen of resistant or susceptible varieties could be traced. Neither could a difference in the quantity of tannin be found; in treating the phellogen cells with $CaCl_2$ the color of the cells of susceptible varieties was much darker than those of resistant varieties.

The question could, however, be looked into by other means. It had been noted that treatment of the tubers with the vapor of alcohol had a distinct influence on the macroscopical effect of an infection. When tubers are kept in a Petri dish in the vapor of ethyl alcohol during 24 hours after having been inoculated in a slit of the parenchyma, the brown coloration characteristic for an invasion by *P. infestans* occurs much later than in control tubers. Invasion by the fungus itself is not in the least retarded. The vapor of ethyl alcohol appears to have a distinct effect on the reaction of the host plant in connection with the invasion by *P. infestans*.

In view of this observation, resistant tubers inoculated on the cork-cambium by a zoospore suspension were brought under the influence of the vapor of alcohol. Twenty-four hours were enough to cause the tubers to be thoroughly invaded. Unwillingly I am producing here an argument for the cause of prohibition. The conclusion drawn is that resistance can be due neither to any anatomical difference in the cork-cambium, nor to any chemical constituent always present in the cells.

In the experiments described above, it is clear that the defensive reaction of the tuber, which comes into play when the fungus enters the tuber tissue of a resistant variety, is inhibited. Narcosis by alcohol prevents this reaction from playing its part.

Now among many varieties tested in field experiments many differences in

the varietal degree of susceptibility of the tubers occurred that were not to be explained by any difference in the behavior of the cork-cambium. The way the fungus invades the tubers had to be looked into to explain these differences. Newly dug tubers were inoculated with a zoospore suspension. After a lapse of 3–4 days early points of infection could be seen as thin livid lines under the intact skin. If a lenticel is present at one end of such a line, this line may be followed up macroscopically to the centre of the lenticel. A great difference was noted in the results of inoculation experiments on one and the same variety that is known as most susceptible when grown in a heavy soil. Among 124 tubers grown in dry sandy soil only 8 infections through lenticels could be noted. There were amongst the clay-grown tubers several that showed over 40 lenticel infections per individual tuber. An examination was made to determine whether any anatomical difference in the lenticels could be traced, and such a difference that can be recognised microscopically was found. When sections through lenticels are stained with Sudan III glycerine, in order to study the degree of suberization of the cell walls, the sand-grown lenticels were seen to be covered by one or more layers of parenchymatous cells with suberized walls. The clay-grown lenticels were lacking in such a covering. Here the middle part is parenchymatous and only where these parenchymatous cells adjoin the phelloderm were the cell walls suberized. It was felt that here was a difference that might account for varietal differences in susceptibility, but to make sure, a method had to be looked for whereby many lenticels might be easily examined. The following method was used:

A lot of unripe tubers of one and the same variety were inoculated by placing them in a spore suspension and the amount of lenticel infections noted. At the same time the skin was removed from a number of check tubers and this was kept in formol for further study. By bringing such a piece of skin as a whole under the microscope and staining with Sudan III the limit between suberized and non-suberized tissue is recognizable. The outlines of all non-suberized areas in several pieces of skin of a same lot were mapped out, using a drawing apparatus magnifying 70 times and a tracing therefrom was made on a paper of uniform quality.

The areas so traced on the paper were cut out and weighed all together. The outlines of the whole pieces of skin examined were similarly traced but in actual size, and these were also cut out and weighed. The ratio between the surface of skin examined for one lot and the surface of all non-suberized parts in the lenticels occurring thereon can now be calculated. When this figure is low it means a great amount of non-suberized lenticels; if high, the reverse. The figures so arrived at are directly comparable for all lots.

For tubers grown in clay-soil of various varieties these figures were compared with the amount of lenticel infections in artificial inoculations. Out of 10 varieties with a ratio figure less than 1000 (minimum 242), meaning a great amount of non-suberized lenticels, in 9 cases the number of infections per tuber was greater than 5; in 5 cases it was greater than 10. The maximum was 23.2, but of varieties with a ratio greater than 1500 (maximum 15876), thus meaning a

small amount of unsuberized lenticels, the greatest amount of lenticel infections was 3.2; in 4 cases the amount was less than 1. The correlation is sufficiently clear for the condition of the lenticels to be regarded as the cause of difference in the varietal resistance in tubers susceptible by means of the cork-cambium.

When the same data were collected for sand-grown tubers the results were less clear. Tubers with a ratio over 1500 behave in the same way as tubers grown in clay soil. The maximum of infections attained per tuber was 0.8. Among tubers with a ratio less than 1000, 2.8 is the highest amount of lenticel infections, a much lower figure than the amount found for clay-grown tubers with the same degree of suberization. Non-suberized lenticels appear to be much less of a danger in sand-grown tubers than in clay-grown ones. Possibly suberization is only the last of a series of changes that succeed quickly in the clay-grown tubers.

It was noted by inoculation with a zoospore suspension that the eyes may also provide a means of entrance. When the results of all inoculation experiments for clay-soil tubers before and after Sept. 1st were put together, it appeared that the amount of infection through the eyes was 5.1 times greater in older tubers than in young ones. For sand-grown tubers it was found that the older tubers gave 10 times as much infection through the eyes as the younger tubers. Thus the danger of infection through the eyes is greater in ripening tubers than in young ones.

Soil conditions appeared to have no influence on the degree of susceptibility through the eyes. Two varieties gave no eye infections, whether they were grown on clay or on sandy soil.

To see whether an anatomical quality might account for these differences the anatomy of an eye was examined. I may state directly that I did not get farther than to determine the method of entrance into a bud, and did not succeed in finding differences in the material available. Microtome sections of the eyes were made. Eyes consist generally of 3 buds, the middle one of which is most advanced in development. The meristematic part of such a bud is covered by outer and inner bud-scales. An outer bud scale is clothed with a phelloderm. In this phelloderm small unsuberised zones may be found, generally with stomata. In the top of such an outer bud-scale the phelloderm generally is absent and the parenchyma is only covered by an epidermis. The inner part consists of a well developed parenchyma with vascular bundles.

The inner bud scales consist of parenchymatous cells with small intercellular spaces; stomata are present but there is no cork-tissue.

When the anatomy of a sound eye was understood, newly infected eyes were sectioned. Thirty-seven infections through the eyes not mutually connected were recognized. In 31 cases the centre of the infection lay in the outer bud-scale; in 4 cases an inner bud-scale contained the infected part, but here the infection could not be followed into the parenchyma of the tuber and in 2 it was not discernible. The meristematic growing-point always was quite intact. In one case the infection was at its very earliest stage and it could be seen that the diseased

tissue corresponded with 2 openings in the outer bud-scale, while the tissue under the third stoma was still sound.

Hence in ripe tubers the path of entry leads through the outer bud-scales which, through openings in the protecting cork-layer, offer the possibility of entrance. The question is obvious whether in younger or resistant eyes any difference in the anatomy of the eye might be found. There, however, the material gathered was not sufficient to provide an answer.

In comparing the results of laboratory inoculations with observations in the field it was manifest that among the 3 qualities tested the resistance in the cork-cambium protects the tubers most satisfactorily. For these tubers the degree of lenticel or eye susceptibility is of no consequence, and soil conditions do not influence the degree of susceptibility. It is important to pay great attention to this feature, if the raising of a variety resistant to late blight on heavy soil is aimed at.

ESSENTIAL FACTORS IN DESTRUCTIVE PLANT DISEASE DEVELOPMENT[1]

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When honored by the invitation to open this discussion the suggested topic was "epidemiology" or "epiphytology." This was evidently a courteous recognition of the fact that so much of our efforts at Wisconsin in recent years has been directed to the relation of environment to disease development (Jones, Johnson, and Dickson '26). Perhaps we might have discussed these problems under the inclusive term of ecological pathology which Whetzel and associates ('16) aptly defined as "that phase in the discussion of a disease which deals with the relation of environmental factors to its occurrence, severity and character." He lists these factors as, chiefly, climatic, soil, and cultural, which may effect the disease indirectly through their influence on the pathogen or the host, or on both.

I prefer, however, for two reasons, to consider these matters with a somewhat broader conception in mind, as suggested in the title. The first reason is that on previous occasions I have treated of the narrower topic of the relation of environment to disease in plants as based on our Wisconsin studies (Jones'24). The second is that analysis of the influences determining the occurrence and severity of plant disease epidemics leads to the conclusion that although environment plays a very important role, there are other essential factors requiring consideration along with environment.

It is, indeed, pertinent that some phases of this general topic should have place on an international phytopathological program, since they are basic to considerations of quarantine measures which involve important international relations. Moreover, the responsibility for leadership in opening such discussions may well rest with "new world" representatives, since it is a matter of common experience that unexpectedly destructive plant disease developments regularly follow man's pioneering ventures in plant culture in new regions.

Pioneers inevitably disturb nature's biological equilibria. The rewards are tempting to the venturesome, but he must often meet calamity in reaching for them. Such pioneering with plant culture has proceeded in the Americas on a scale which peculiarly combines the extensive with the intensive. That is to say, with a relatively limited background of experience, we have repeatedly ventured to devote great areas of land to the intensive growing of a narrowly limited variety of crops or even have been tempted to go dangerously far in one-crop

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culture.[2] Where practicable, experience should precede and may partially safe-
guard such large adventure for two reasons obvious to pathologists, whether
students of plant or animal disease. In the first place, the outcome is problem-
atical when new or untried races or types of potential host organisms are exposed
to the attacks of new or untried potential parasites. In the second place, the
introduced organism—whether host or parasite—may react in quite unexpected
ways to new environmental influences. Time as well as human experience are
essential for the restoration of such disturbed biological equilibria whether the
stabilization processes proceed more slowly through natural selection or more
rapidly when aided by scientific leadership.

Citrus canker, fire blight, San Jose scale, and Mediterranean fruit fly explain
in part the especial concern of such territories as Florida, California, and Hawaii
quarantine matters. The burned child dreads fire. And our northern States and
Canada have learned the serious possibilities of chestnut blight and pine rust
as well as of potato wart, not to mention the corn borer. But no country is
exempt. Europe even earlier learned the possibilities of destruction from Ameri-
can parasites of potato and vine. Some international as well as more localized
quarantine measures regulating or restricting plant shipments must therefore
be maintained in order to lessen such inevitable dangers. Most will doubtless
agree, however, that while supporting quarantines we must not rely upon them
unduly. The element of human judgment must always enter into their execution
as well as formulation and at best they cannot be perfect or absolute. Nor should
they be regarded as necessarily permanent for any specific parasite. I think
most of us will agree that experience to date shows little basis for hoping for even
local extermination by human effort of any well-established and well-adapted
plant pest. If so, then it seems to me inevitable that the constantly increasing
maze of interregional commerce and migration will surely tend toward wider and
wider spread of such parasites. In other words, the factors determining the
ultimate worldwide distribution of plant pests, especially the fungous diseases
of plants, are primarily those concerned with the distribution of susceptible hosts
under an environment favorable to the parasites. This may sound pessimistic
but I do not myself conceive it in that spirit. Rather is it the formulation of
another challenge to plant pathologists of the present and the future comparable
to those which have always been adequately met in the past. Repeatedly neces-
sity must and will become "the mother of invention." The essentials in environ-
mental relation are capable of analysis, and plants are wonderfully plastic when
molded by the sympathetic hand intelligently directed. But it is important to
remember that a primary condition in preparing to meet such a challenge is to
define the problems involved as promptly and as clearly as may be. Until this
this is done progress will be slow and erratic. When it is done we cannot doubt

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[2] Examples of this are afforded in the great spring wheat areas of northwestern United States
and adjacent Canada, in the cotton belt of the southeastern states, and in the citrus regions of both
Florida and California. The writer was even more deeply impressed by the magnitude, not to say
temerity, of such plant cultural ventures during recent visits to the sugar cane fields of Cuba and the
corresponding cane and pineapple plantations of Hawaii. In all of these situations the desire is to
continue the cultivation of a single crop plant on the same soil without rotation.

the outcome. There is nothing so stimulating to youth as the conviction that definite work awaits its doing, and no matter how rapidly some of us age, youth is ever waiting at hand. Its one eager desire is that experience point the way, defining the best-worth-while tasks.

If we are to attempt this for the problems in hand I would wish to begin with what I consider the phytopathologists first axiom. It is that three fundamental elements require consideration for each infectious disease, the pathogen, the host, the environment. Each presents its own peculiar aspects of the problem although in many cases these are closely interrelated. One might, therefore, proceed to discuss our topic, the destructive factors of plant disease development, under these three heads. If, however, one seeks to analyze specific problems in the field of epidemiology and evaluate the important variables which may influence such disease development it seems simpler to consider the details under headings which relate as closely as practicable to the chronological sequence of the events involved. With this idea in mind, for any specific infectious disease one may in natural order first give detailed consideration to the pathogen, including its occurrence and dissemination and also its nature and characteristics; host infection naturally follows eventuating, if successful, in the development of the disease to host tissue injury and of the pathogen to natural maturation. While it is evidently artificial thus sharply to segregate or classify the complex and involved relations of host and parasite as influenced by environment; nevertheless, it seems that only by so doing may we successively focus attention upon certain outstanding factors which deserve consideration.

With this analysis in mind let us review some familiar epidemic diseases seeking evidence as to the relative significance of these things in particular cases.

The Occurrence and Dissemination of the pathogen, the First Essential

The recent spread of the Asiatic chestnut blight fungus (*Endothia parasitica*) in the eastern United States seems to have proceeded steadily with only minor variations in rate or severity until its occurrence is co-extensive with the host range. Its destructive march has apparently met with no marked check from climatic variations nor have any regions excaped invasion. It appears that the introduction of the pathogen was the factor of essential importance in this case. Whatever the variations in regional dissemination, in host susceptibility, or in relation of environment to disease development these were of minor influence.

The same thing may in part be said of the European asparagus rust (*Puccinia asparagi*) which preceded the chestnut blight by about a decade in its epidemic spread across the United States. With this rust the remarkable thing was the rapid rate of dissemination. Apparently wind-borne, it went in epidemic severity from the Atlantic to the Pacific in some five years, an apparent spread over some five hundred miles per season. When this new asparagus parasite reached California, however, Smith ('05) soon detected that under the peculiar coastal climatic conditions its destructive prevalence is definitely related to certain climatological factors. Where the air remains dry, or even with oc-

casional rains, there is little damage, but the amount of rust varies directly with the amount of dew.

Perhaps even more interesting because of the more complicated biological relations involved are the recent revelations concerning the dissemination of certain insect transmitted virus diseases. In the western United States the curly top disease of the sugar beet appears to be endemic, and it occurs to some degree every year. So far as demonstrated, its dissemination in nature is wholly dependent on one insect, the beet leaf hopper (*Eutettix tenella*). Disease epidemics, in this case are, therefore, definitely conditioned upon the occurrence and migratory flights of this leaf hopper. Ball ('17) has shown that this insect vector may fly in immense swarms for long distances, and over even the higher western mountain ranges. The disease may thus be suddenly introduced over wide areas in epidemic proportions.

Kunkel ('26) has more recently shown that the "yellows" disease of China asters and other plants is a virus disease and that, like the beet disease, epidemics of this malady are conditioned upon a leaf hopper as carrier. Here again we are apparently dealing with an endemic virus and likewise only one insect, *Cicadula sex-notata*, is known to act as vector for the aster yellows. This leaf hopper is native of Europe and doubtless there feeds on the China aster as in America; but aster yellows is unknown there, probably because the virus has not yet been introduced. Neither is the disease reported from Asia. Possibly even if the virus were taken to the Orient it might not spread if this insect were not there present. To summarize then, for this aster yellows disease, the complex problem of epidemiology involves an American virus, an Asiatic host and a European insect vector. Apparently it is only when this specific virus, this single insect carrier, and susceptible host plants meet under favoring environmental conditions that the disease epidemic may occur. When, however, these factors properly coincide there results a disastrously destructive disease. Probably further study will reveal numerous like examples among these serious but puzzling viroses. And, with many potentially serious introduced diseases of other types, the factors relating to subsequent dissemination may be almost as significant as those dealing with the original introduction.

The Nature and Characteristics of the Pathogen Also Important

Formerly the conceptions of species as applied to fungous pathogens were even more broadly inclusive than with hosts. It is, however, over thirty years since Eriksson ('94) in Sweden demonstrated the occurrence of specialized races or forms among the cereal rusts. Almost continuously since the evidence has been increased along this line, notably by Ward and Salmon in England, Fischer in Switzerland, Reed, Mains, Stakman and associates in America. Each year now we are taught to expect perplexingly detailed reports upon the significance of such races or forms in relation to epidemiology. It seems demonstrated, for example, that specialization with the stem and leaf rusts of grasses has proceeded to such a degree that a rust epidemic upon any graminaceous host is absolutely

conditioned upon the presence of one or more of those narrowly specialized races which can attack that particular host. Moreover, recent evidence from various sources supports the idea that similar specialization may occur commonly, not only with the rusts but with the smuts and other long familiar parasites.

The multiplicity and variety of this evidence, indeed, raise most perplexing questions for us old-school pathologists. Must we not again pass on to the younger generation the challenge? Dare we longer assume that the traditional species concept of any parasite is a safe guide as to its possible pathogenic range? Must we not urge persistence in the painstaking survey of this whole problem in parasitology including not alone the higher fungous parasites, but the corresponding and equally fruitful fields of research in bacteriology and the even more "up-to-date" challenges in what we perhaps may be permitted to term "virology"?

Host Infection

In many cases we know that virulent types of the potential pathogen may be present and even widely disseminated yet no serious disease occurs. Here it is that the possible influence of environmental factors deserve critical consideration. To illustrate how dominant these may be, we may cite some evidence from recent studies in our laboratories dealing with two familiar and highly aggressive soil-borne diseases, the onion smut (*Urocystis cepulae*) and the cabbage club root (*Plasmodiophora brassicae*). Each is caused by an introduced parasite which is already widely disseminated in the United States and is insidiously invading new territory. As evidencing this I can bear personal witness, since I followed such advances in New England some three decades ago and in the last two decades have witnessed both diseases rapidly invade intensive truck growing districts in Wisconsin. Once established under suitable environment, each persists to plague the growers indefinitely for future years. But in both cases alike the organism may be present in the soil where the host is planted and little or no disease may occur. This results from the fact that both of these potential parasites are even more sensitive to certain environmental factors than are their respective host plants.

With club root, which has long been known to be sensitive to soil reaction, Monteith's ('24) recent studies have shown in addition that the parasite requires a relatively high soil moisture content for its aggressive development. If the soil about the roots is dry, therefore, there may be little or no club root on cabbage, even in old infested fields, probably because abundant soil moisture is necessary for the spore germination and soil migration of *Plasmodiophora*. This accords with Ravn's ('19) earlier observations in Denmark that low-lying areas and land that is poorly drained favor the development of the disease, and Cunningham's ('14) demonstrations in Vermont that "hilling up" cabbage plants is an effective control measure.

With onion smut Walker and Jones ('21) have again shown that environment (in this case soil temperature) may have a dominant influence upon the geographic distribution of disease occurrence as well as upon its local severity. High

soil temperature during the germination period of the onion may operate entirely to prevent the occurrence of the disease even in smut-infested soil. To understand this one must recall that the onion smut fungus produces abundant long-lived resting spores, or spore balls, in the smutted bulb scales which are disseminated with the dormant bulbs. Where onion sets are grown in smut-infested soil, as is very commonly the case, the fungus is widely disseminated wherever small bulbs are replanted. The smut spores may persist indefinitely in the soil, and Anderson ('12) has shown that the fungus may even increase as a soil saprophyte. The infection of onion seedlings ordinarily occurs only through the young subterranean part of the cotyledonary leaf, hence is restricted to the first two or three weeks following germination. Although the young onion develops best at rather cool temperatures, 10–18°C., it will come along fairly well at soil temperatures up to 30°C. or even above. The smut fungus is distinctly a low temperature organism and much more sensitive to high temperatures than the onion plant. Its optimum is about 16°C. as determined for spore germination and mycelial growth as well as for host infection. When the temperature rises above 20°C. the fungus is soon progressively inhibited and is entirely checked at about 27–28°C. As a result, if the onion seed is planted in such warm soil and germinates at uniformly high temperatures it escapes the disease because the smut fungus, no matter how abundant in the soil, will under these conditions be unable to germinate or at least to parasitize the seedling seriously. What, now, is the relation of these facts to the geographical occurrence and severity of the onion smut disease? Onion smut as an introduced fungus, probably disseminated by onion sets, has spread rapidly across the northern United States from the Atlantic states westward to the Pacific coast. It is, however, unknown in the great commercial onion districts of Texas and Louisiana. Smutted onion sets are shipped into these southern districts annually, often by the carload. Why has not the disease become established and destructive? For the simple reason that in the South the onion is grown as a winter crop. The seed is planted in late summer or early autumn when the soil temperatures are continuously so warm as to inhibit the development of the parasite until after the onion seedling passes the susceptible stage.

These examples were selected because of their simplicity in illustrating the point that the permanent distribution and destructive occurrence of a parasitic disease is conditioned not alone on the initial introduction or subsequent dissemination of the parasitic organism but quite as clearly upon the influence of the environmental factors which thereafter surround it, season by season. This statement must be accepted as axiomatic in plant pathology, but thus far our analysis of the relation of the various limiting environmental factors has been fragmentary and inadequate. We have, in our studies with the Wisconsin soil temperature tanks (Jones, Johnson, and Dickson '26), found that the cabbage yellows (*Fusarium conglutinans*) and all the allied vascular *Fusarium* wilts studied (flax wilt, tomato wilt, pea wilt, etc.) are high temperature diseases and are sharply inhibited by low temperatures. Certain other common soil parasites cause, by contrast, low temperature diseases, for example, the *Thielavia* root

rot of tobacco, etc., (*Thielavia basicola*) and the *Rhizoctonia* stem canker of potato, etc., (*Corticium vagum*).

It would be a serious omission were one, by thus referring to the simpler aspects of these problems, to distract attention from the inherent complexity of the relation of environment to disease. One must in the analysis of each case recognize that this relation involves the reactions of both parasite and host to varying factors. Moreover, even though we may find a single factor of significant importance in many cases, nevertheless the constant interrelation must be recognized of the several variable factors including, for the soil-borne diseases, temperature, moisture, light, nutrition, soil reaction. Dickson ('23) has recently shown for the seedling blight of cereals (*Gibberella saubinetii*) that not only may these things influence the parasite but that the degree of host invasion may be directly influenced by any combination of environmental influences which materially affects the rate or character of host metabolism.

Our experimental studies at Wisconsin upon the relation of environment to disease have been thus far primarily restricted to the soil-borne parasites.[3] It is, however, obvious that the relation of environment to the regional occurrence and destructiveness of aerial parasites would be even more important. It is well known how significant are such climatic influences with the rusts, powdery mildews, and downy mildews. The dependence is apparent of all these upon atmospheric moisture adequate for spore germination. Over a decade ago Melhus ('11) found that with the white rust of crucifers, *Cystopus candidus*, normal spore germination and consequent host infection could only be secured at a chilling temperature, about 10°C. being especially favorable.

DEVELOPMENT SUBSEQUENT TO INFECTION

It is also a matter of common experience with these parasitic diseases that environmental factors have much influence upon development subsequent to infection. We may cite two quite different types of result from repeated personal experiences with two diseases.

The first of these, cabbage yellows, is caused by a soil fungus (*Fusarium conglutinans*) which may occur abundantly and uniformly distributed in old cabbage fields in Wisconsin. As a result, even with our special resistant cabbage varieties like Wisconsin Hollander,[4] if the temperature in July, immediately

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[3] The relation of environment, especially moisture and temperature, to the parasitic attacks upon aerial organs, foliage and fruit, must always have been evident to every thoughtful observer. The inherent difficulties of conducting critical experiments to measure or define what these are with reasonable accuracy are, however, quite serious. This in part results from the obvious fact that it is almost impossible to vary one factor in the environmental complex without disturbing others, perhaps equally influential. While this holds in some measure for soil-borne diseases it is rendered peculiarly pertinent for studies upon the diseases of aerial parts because of the importance of light relations which so greatly complicate any efforts at critical work on the relation of environment to disease in the case of aerial plant parts. For this reason all our earlier efforts were directed to the simpler problems of soil-borne diseases (1) Latterly, however, our associates, especially Dickson (13) and Keitt (22) have successfully turned to certain problems involving the aerial relations.

[4] For details concerning this *Fusarium* disease of cabbage and its control through the use of disease resistant strains, see publications by L. R. Jones, J. C. Walker, and associates (lit. cit., Jones and Walker '15, Jones *et al* '25, etc.).

following cabbage transplanting, is warm the fungus development is so favored that all susceptible varieties succumb and a large percentage of even the resistant strains may show incipient disease. If, however, as commonly occurs in Wisconsin in early August, the nights become cool and the soil temperature drops, these cabbages even though slightly infected recover and mature practically normal heads. It is to be noted that in this case the influence of environment was either upon the initial infection or the subsequent destructiveness of the disease in plants so parasitized and had nothing to do with dissemination.

The second example I would cite is the familiar potato disease caused by *Phytophthora infestans.* In the northern United States there is no evidence that this persists in the soil.[5] Instead, we conclude that it overwinters and is disseminated only in a limited way in potato seed tubers. The sporulation of the mildew upon the young shoots arising from these in early summer as shown by Melhus ('15) gives a few localized centers of infection. If the weather conditions are dry and hot such sporulation may be very limited and little or no secondary spread results. If, however, there occurs at this time a period of a week or more of fairly continuous moist weather with rather cool night temperatures, which with this fungus (Melhus, '15a) as with *Cystopus* favor normal zoospore formation, the parasite will be rapidly and widely disseminated in the field. Secondary and even tertiary host infections occur, increasing rapidly in geometric ratio, since under favoring environment renewed sporulation may follow within five days of leaf infection. Thus from a very limited number of initially diseased plants this mildew may in a fortnight or so develop to an epidemic stage covering indefinitely extensive territory. It is to be noted that, with such aerial parasites as the mildews and rusts generally, the influence of environment operates quite differently than it does with the soil-borne parasites like the cabbage *Fusarium* cited above or the similar *Thielavia* and *Rhizoctonia* diseases. With these soil-borne organisms environment relates chiefly to primary infection and subsequent host destruction, while with the aerial parasites, by contrast, environment relates more influentially to fungous sporulation and dissemination and thus to secondary and tertiary infections.

The terms "epidemic" or "epiphytotic" are more clearly applicable to the diseases of this latter class. The dominant influence of environment upon the destructive occurrence of soil-borne diseases has, however, been demonstrated to be quite as direct and, economically, scarcely less significant.

Perhaps these analyses of experience with two such destructive disease types of widely differing nature may properly preface the point which I wish to emphasize above any other in this paper. It is this: With maturing experience in the evaluation of plant disease problems I have less interest than formerly in

[5] Recently some very interesting work has been done in Holland by deBruyn ('22) and Löhnis ('22, 24), on the relations of host and parasite and the influence of weather conditions upon epidemic occurrences, including persistence from season to season of *P. infestans* in the soil, or otherwise. These well emphasize the importance of intensive local studies of familiar parasites which may behave very differently under such widely different climatic conditions as prevail for example in northeastern Europe and in the northern Mississippi Valley.

the early type of pioneering work, such, for example, as the description of new parasites of minor significance, the sparsely annotated surveys as to the occurrence of plant diseases, or the undiscriminating cataloguing of the parasites occurring on a particular host. All of these record useful information but of relatively minor phytopathological significance. The thing, by contrast, which increasingly impresses itself upon me is the highly significant difference in the seasonal or regional occurrence and relative destructiveness of our long familiar parasitic diseases. It seems evident that we should increasingly recognize, in America at least, that whatever, may have been our earlier responsibilities as phytopathologists, the days of this type of pioneering are past. One of our most important immediate duties is to face the present day challenge to make critical restudies of our more common and familiar plant diseases, trying thus to learn the essential factors determining the seasonal or regional variations in their destructiveness. Only in this way will we adequately get at the fundamentals of our science, on the one hand, or best contribute to practical control measures on the other. In order to indicate the method and illustrate both the difficulties and the worth-while-ness of its prosecution I have sought the cooperation of my associate Dr. G. W. Keitt in summarizing his recent work on the epidemiology of apple scab (Keitt and Jones '26) caused by *Venturia inaequalis*.

WISCONSIN STUDIES OF THE EPIDEMIOLOGY AND CONTROL OF APPLE SCAB

These studies have been conducted by Dr. Keitt and his younger associates in Wisconsin orchards and in our laboratories and greenhouses for some eight seasons. Early in the work the desirability of a better understanding of the development and the prevention of epidemics became apparent. Consequently, effort was directed along two major lines: (1) field studies of the development and the control of the apple scab disease in relation to the natural environment and (2) laboratory and greenhouses studies of the development of the disease and the action of certain fungicides, with special consideration of the relations of factors of the environment, to these processes.

In the field studies the seasonal development of the scab pathogen, the host plant, and the disease were traced in detail in relation to meteorological conditions and to the effectiveness of various control programs. In so far as feasible, data were taken on a quantitative basis by standardized procedures designed to facilitate tabular or graphic summarization and correlation. While quantitative methods and statistical presentation were thus employed, it is clearly recognized that the results must be interpreted as semi-quantitative, in view of the many variables which are concerned in biological problems of this type. A meteorological station equipped with standard instruments was established in the experimental orchards. By this means hourly records of air temperature, relative humidity, rainfall, wind velocity, and sunshine were obtained. For grosser comparisons and correlations, graphic summaries of the type shown in Figure 1 were developed each year. In order to facilitate more detailed analysis, bi-hourly averages of the meteorological data were tabulated in relation to the

frequencies of ascospores in the orchard air, as determined by a specially devised filtration technique (see Fig. 1). Control experiments included about 250 plot treatments. Statistical data from these plots were tabulated and studied in correlation with the results from the other lines of work.

The laboratory and greenhouse experiments were designed to seek further light on the processes of spore germination and infection, and on some relations of environment to the development of the disease and to the effectiveness of certain fungicides. A large infection chamber was devised, in which a saturated atmosphere could be maintained throughout a suitable range of approximately constant temperatures. Potted apple trees were subjected to infection by naturally discharged ascospores of *V. inaequalis* from wet leaves suspended in the upper part of this chamber. The spores germinated in condensation water on the leaves under conditions very closely simulating those of infection periods in nature. After the plants were removed from the infection chamber, they were subjected to varied environments.

In the light of the results of the field and laboratory studies it was sought to analyze the development of scab epidemics and to define critical periods in relation to their occurrence and control.

Under Wisconsin conditions the apple scab fungus was found to overwinter to a significant extent only through the formation of the perithecial stage in dead leaves. Ascospores appear, therefore, to constitute the only important source of primary inoculum in this state. Consequently, a detailed knowledge of the rôle of the ascosporic inoculum seemed to be of much potential importance in relation to epidemiology and control. Mature ascospores were ordinarily observed by the time the first susceptible tissue was exposed in the unfolding "fruit" buds. They were discharged only when the leaves were wet. The periods during which ascospores were discharged in each season varied from about five to nine weeks. The maximal concentration of ascospores in the orchard air, as revealed by the filtration technique, was nearly 300 per cubic foot. Frequencies of from 20 to 100 ascospores per cubic foot of orchard air were not uncommon during the height of the season of discharge.

Primary infection commonly occurred during the first sufficient rain period following the exposure of susceptible host tissue in the unfolding "fruit" buds, except in seasons when spring drought delayed the maturity of ascospores. The apical portions of sepals and leaves were found to be the first susceptible host parts exposed. The sepals were the most exposed parts of the "blossom" buds during the early stages of their expansion. Early sepal infection places the fungus in a peculiarly favorable position for local infection of the adjacent surface of the affected blossom or young fruit by conidia, which are produced in abundance upon the primary lesions on the sepals. These conidia, which persist tenaciously on their conidiophores when dry, are readily detached in meteoric water, which is the chief medium for their dissemination in nature. In years of severe scab epidemics it was not uncommon to find sepal infection on 75 per cent or more of the blossoms of certain varieties of apple in the experimental orchards. A comparative study of sepal-infected and sepal-clean fruits showed that scab develop-
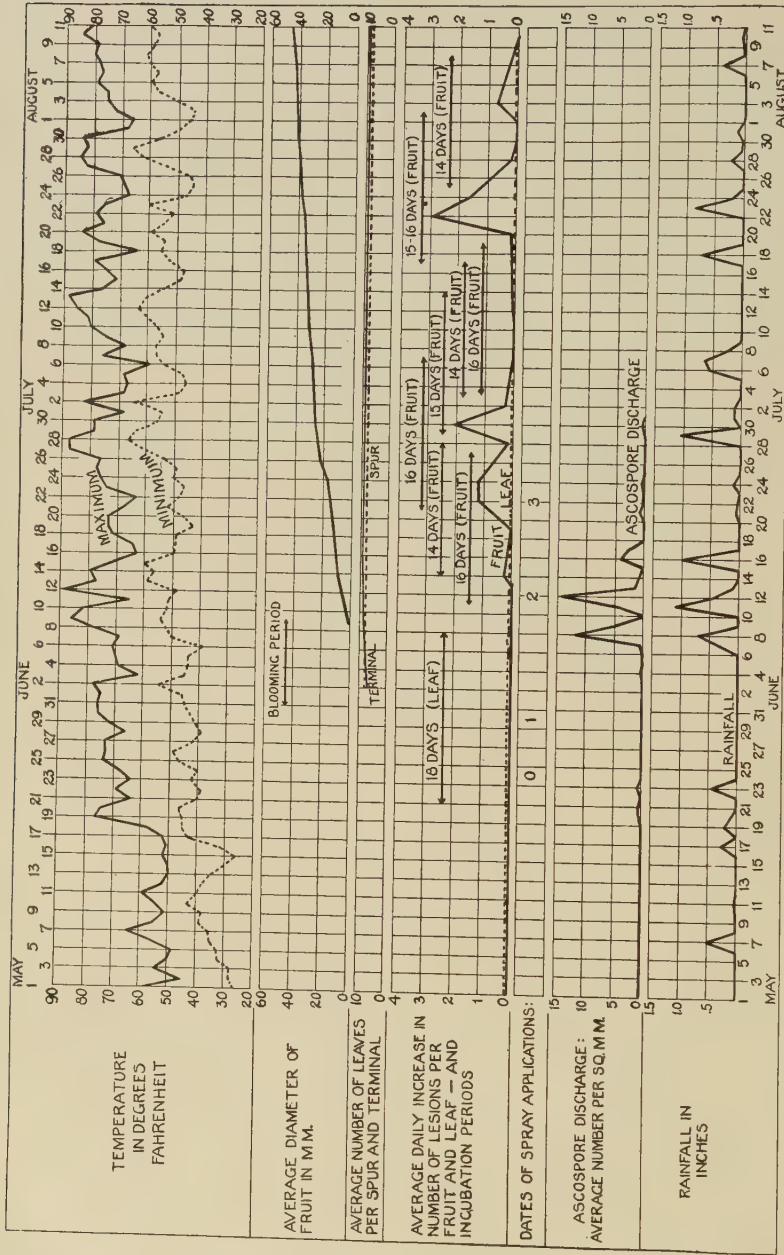
Fig. 1.—A graphic summary of certain records relating to the epidemiology and control of apple scab, Sturgeon Bay, Wis., 1920.

ment was far more serious on the fruits which had sepal infection. The severe infections which led to one-sided development of the fruit were commonly traceable to local secondary infection by conidia from lesions on the sepals. Furthermore, in 1924, when the fungicidal programs failed because of abundant very early sepal infection prior to the first treatment, the disease was well controlled on those fruits which did not have sepal infection. It is apparent, therefore, that early sepal infection is of much importance in relation to epidemiology and control of this disease through establishing the fungus in a remarkably favorable situation for secondary infection of the affected fruit during the period of its greatest susceptibility and at a stage when thorough protection by fungicides is difficult.

The results of these studies show that the timeliness and amount of primary infection are of cardinal importance in the development of difficultly controllable epidemics. In years of sparse primary infection the disease developed in mild or moderate degree and was easily controlled by almost any of the fungicidal programs used, while in seasons of early and abundant primary infection severe epidemics developed and all control programs failed, except those especially designed to prevent the early infection.

The field studies showed that abundant conidia for the secondary inoculum were never lacking on unsprayed trees after infection was well established. Two especially important phases of secondary infection were shown to be (1) local infection of young blossoms or fruits by conidia from sepal infections and (2) the establishment of the fungus in the leaves, especially through inconspicuous late-season infection of the dorsal surfaces, thus making possible the development of a more abundant ascosporic inoculum for the following season.

The most critical period for the development and control of scab epidemics was found to extend from the time the apical parts of the sepals are first exposed in the opening "fruit" buds to an indefinite time some two to four weeks after petal-fall. The early part of this period is the more critical; because (1) the scab fungus has a comparatively long incubation period, (2) the host passes rather rapidly through its period of maximal susceptibility, (3) environmental conditions are likely to be more favorable for early than for later secondary infection, and (4) the rapid expansion of host parts, especially the leaves, in the pre-blossom period makes it difficult and expensive to keep them adequately protected by fungicides. In cool climates, as in that of the Sturgeon Bay district of Wisconsin, important periods of secondary infection may occur at any time during the season. A notably critical period occurs in the fall, when cool moist weather ay make possible severe fruit infection and the abundant establishment of the fungus in the leaves, particularly in the dorsal surfaces. If primary infection has been adequately controlled, however, the disease is easily held in check in the later stages.

The results of the control experiments harmonized with and contributed to the data on epidemiology. The timeliness, thoroughness, and frequency of fungicidal applications seemed to be more important in relation to control than the material used. It was apparent that programs of applications should be

modified in accordance with the adaptations of the fungicide and the require-ments of local conditions. The importance of adequate treatments in the critical pre-blossom period was strikingly manifest in years of epidemic development. A critical study of the development of the disease in relation to fungicidal treat-ments showed clearly that the problem of scab control on the fruit is quite differ-ent from that on the foliage. The blossoms, and later the fruits, of a given va-riety develop so nearly simultaneously that they may be protected satisfactorily with a practicable number of treatments. The leaves, however, being expanded in succession during a considerable period are continually exposing unprotected tissue during the intervals between applications in the period of leaf growth. Consequently, in the presence of an abundant ascosporic inoculum and favor-able conditions for infection, the problem of controlling scab on the leaves by use of fungicides is comparable in its difficulty to a like control of apple rust (*Gymnosporangium juniperi-virginianae* Schw.). It is apparent, therefore, that the spray programs now in general use are adapted primarily for the control of the fruit, and do not adequately safeguard against leaf infection and the recur-rent development of an ascosporic inoculum for the following year. In view of these facts and of the great importance of the ascosporic inoculum in the development of difficultly controllable epidemics, special attention has been given by Keitt and Wilson to the possibilities of preventing the abundant production and timely discharge of ascospores. The post-harvest period prior to leaf-fall has seemed to cover a potentially vulnerable period in the life-history of the fungus to which comparatively little attention has hitherto been given. There-fore, a fungicidal treatment has been sought, which applied after harvest but before leaf-fall, would economically prevent or limit the production of ascospores, without serious host injury. While the results of this work are, as yet, incon-clusive, they seem to be sufficiently encouraging to justify continuation of the experiments. In connection with this phase of the problem, a study of the development of the ascigerous stage of the scab fungus in nature in relation to certain factors of the environment has been made by E. E. Wilson (in process of preparation for publication[6]). This work, which cannot be discussed in detail because of limitations of space, has thrown much light upon many hitherto obscure phases of the development of the ascosporic inoculum in relation to epidemiology.

Conclusions

I have thus reviewed in some detail these Wisconsin studies on the epidemi-ology of apple scab in order to illustrate the methods as well as the general desir-ability of seeking a more adequate understanding of the development and con-trol of diseases, and inquiring into the extent, causes, and effects of their vari-ability. We need to recall again in closing, that adequate approach to these complex problems must be found through as detailed pictures as practicable of the full cycles of development of the pathogen and of the host. From these we

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[6] Wilson, E. E. Studies of the ascigerous stage of Venturia inaequalis (Cke.) Wint. in relation to certain factors of the environment. Phytopath. **18:** 375–418. 1928.

will be enabled to follow with understanding the progressive development of the disease and intelligently direct control measures. It is only on the basis of a sufficient knowledge of these processes and of their variability that we may hope to arrive at satisfactory analysis and solution of our present-day problems of plant pathology, whether we consider them in relation to fundamental concepts in biology or in more immediate application to disease control. It must be clearly recognized, however, that with none of these factors are we dealing with constants. Each of them is a variable in the biological equation. In the present paper, quite inadequate discussion has been given to the possible variations in either host or parasite. In our Wisconsin studies, which are to be regarded only as reports of progress on these complex problems, time has not as yet permitted adequate consideration of the possible racial or other variations of the pathogens involved. We have, however, found abundant evidence of the corresponding host variations ranging from extreme susceptibility to relative resistance or possible immunity to parasitic invasion. We have found these in turn to be either temporarily influenced by environment or genetically so stable as to warrant faith in the enduring worth of resistant strains as a factor in disease control.

If I have given you the picture of the phytopathologist's problems as I vision them, you will then agree with me, I believe, as to the complexity of the situation which must be faced when we thus attempt to analyze the essential factors in destructive plant disease development. These problems, which can be met only by re-studying each of our major diseases, are believed to constitute one of the most important present-day challenges in plant pathology.

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ACTION DU PARASITE SUR LA RÉSISTANCE DU CHONDRIOME-PLASTIDOME, SA FRAGILISATION ET L'ALTERATION DE LA STRUCTURE CELLULAIRE[1]

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Nous donnons ci-dessous un aperçu des conclusions que nous croyons pouvoir tirer de recherches poursuivies depuis plusieurs années[2] sur l'effet qu'exerce le parasite (champignon) sur l'architecture interne de la cellule. Les récents progrés de la cytologie (Dangeard, Guilliermond, Cowdry, etc.,) permettent de pousser plus loin qu'on avait pu le faire les investigations dans cette voie. Dans l'étude des effets du parasitisme on n'avait guére considéré jusqu'ici que le noyau parceque la technique ne permettait pas d'aller au-delà. Dés qu'il nous sera possible nous publierons des figures tirées de la documentation graphique déja importante que nous avons établie.

La Résistance Mitoplastidaire Dans La Plante Normale

La résistance des mitoplastes et des mitaplastes[3] aux actions osmotiques et aux autres actions physico-chimiques peut être variable suivant les espéces de plantes et, dans une même plante, suivant les tissus. Les principaux réactifs que nous avons employés pour mettre à l'épreuve cette résistance sont: la saponine, l'eau distillée, le saccharose, le chloroforme, l'éther, la lécithine, l'acide acétique, divers fixateurs.

La Résistance Mitoplastidaire Chez Les Plantes Parasitées

L'action d'un parasite peut avoir pour effet de fragiliser les mitochondries et les plastes (1er stade); si l'action s'accentue ou simplement persiste, leur destruction se produira (2eme stade). Si l'action se maintient au premier stade, la fragilisation, non morphologiquement apparente, peut être mise en évidence

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[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 19, 1926.

[2] Beauverie, J. La résistance plastidaire et mitochondriale et la parasitisme. Compt. Rend. Acad. des Sci., 9 mai 1921. (Cf., au même sujet—Revue d'Auvergne, 1921, 16 p., 1 pl.)

[3] Nous appelons par abréviation "mitoplastes" les mitochondries qui evoluent en plastes et "mitaplastes" les mitochondries qui n'évoluent pas en plastes, ce sont les mitochondries non plastogénes. On les désigne souvent sous le nom de "mitochondries inactives" dans la photosynthése. Nous répudions ce terme trop précis pour des organites dont on ignore encore le rôle. On sait, par ailleurs, combien la terminologie cytologique est pour le moment embrouillée et discutée bien qu'au fond l'accord ne soit pas loin de se faire entre les protagonistes de ces études. Nous ne voulons nullement prendre parti quant au fond et nous adoptons les noms ci-dessus qui nous paraissent commodes, et suffisamment représentatifs.

par l'effet de diverses solutions hypo- ou hypertonique. Nous avons cité ci-dessus les principaux réactifs que nous avons employés. Nous avons reconnu l'intérêt particulier de solutions de saponine (de 1 % à 1 pour 10000). On peut déterminer par tâtonnement un degré de dilution qui détruise les mitochondries et les plastes dans la région parasitée alors que ces éléments restent encore plus ou moins inaltérés dans les parties saines. Il faut toujours compter avec le rôle particulier des diverses membranes qui peut donner parfois au phénoméne une apparence d'irrégularité.

Perturbations De L'Équilibre Osmotique Engendrées Par Le Parasite

En derniére analyse, l'action destructrice du parasite se raméne, le plus souvent, à un phénoméne de perturbation osmotique. Le champignon qui a pénétré dans les tissus y puise de l'eau, surtout quand ses fructifications apparaissent à l'extérieur devenant alors le siége d'une transpiration active. Il en résulte la concentration du suc cellulaire et une déshydratation du cytoplasma. Le champignon peut exercer une action indirecte, par exemple en sécrétant des diastases: sous leur action, de grosses molécules de substances colloïdales: amidon, albumines, etc. sont dédoublées en molécules plus petites, plus nombreuses et cristalloïdes. Il en résulte un brusque accroissement de pression osmotique, une hypertonie dont le retentissement sur le chondriome-plastidome peut être immédiat.

Dans le cas de la maladie de "l'enroulement" de la pomme de terre (Fig. 2), l'amidon se formant dans les feuilles mêmes, par la polymérisation des sucres issus de la photosynthése, la pression osmotique se trouve trés abaissée par rapport à la normale, il y a hypotonie et "fragilisation" frappante des chloroplastes car ils cédent (éclatent aprés s'être transformés en vésicules), sous l'action de l'eau ordinaire, en quelques minutes.

Nous sommes donc amené à parler de l'effet des liquides anisotoniques sur les mitochondries et sur les plastes.

A. Observation Vitale
ACTION DES LIQUIDES ANISOTONIQUES

Sur les mitochondries et les leuco et chromoplastes. La connaissance de cette action est nécessaire pour se rendre compte de l'effet du parasite. On sait que les mitochondries et les chromoplastes (plastes xanthophylliens) et sans doute aussi, les leucoplastes, sous l'influence d'un liquide hypotonique, se transforment en vésicules avec granulations périphériques; la vésicule se rompt, les granulations restent quelque temps éparses puis se fusionnent. Il subsiste, en fin de compte, des granulations assez grosses et peu nombreuses; elles sont trés colorables par la méthode de Regaud et l'hématoxyline ferrique.

L'action, sur ces mêmes éléments, de liquides hypertoniques a été bien étudiée au point de vue cytologique par Guilliermond dans le cas particulier de la fanaison (1919). Celle-ci entraine la déshydratation et un effet d'hypertonie et de plasmolyse (Matruchot et Molliard). Nous rappelerons seulement que la

plasmolyse améne la désorganisation du vacuome, le cytoplasme se confond avec le suc vacuolaire sous forme d'un précipite granulo-alvéolaire, c'est la mort. A ce moment seulement l'eau pénétre et vient produire la vésiculisation des éléments du chondriome. Cette transformation en vésicules résulte donc, dans ce deuxiéme cas, d'une réhydratation *post mortem* succédant à la déshydratation plasmolysante. L'hypotonie succéde à l'hypertonie et, par suite, la vésiculation à la contraction.

Nous avons vérifié ces faits par l'action de diverses solutions agissant sur des tissus vivants: épidermes de pétales de Renonculacées (Renoncules, Ficaire, *Caltha, Trollius,* etc.); ces matériaux, avec leurs chromoplastes à xanthophylle, présentent le méme intérêt, à certains points de vue, que l'Iris et la Tulipe auxquels Guilliermond s'est particuliérement adressé. Nous avons encore experimenté avec des épidermes de feuilles, etc.

Nous n'avons pu saisir la vésiculisation des mitaplastes si abondants dans les feuilles de Ficaire ou de Seigle, par exemple, où on les voit, dans les feuilles adultes, entourant les chloroplastes.

Sur les chloroplastes. A l'encontre des éléments précédents, les chloroplastes se vésiculisent rarement. Nous avons pu, à ce sujet, vérifier et étendre les observations de Guilliermond portant sur le cas particulier des bractées de l'Iris (1919, p. 125, pl. 33). Il se produit une dégénérescence graisseuse de ces éléments. Au moment où elle va commencer, les chloroplastes sont dépourvus de graisse ou n'en montrent que trés peu. Mais, bientôt ils se remplissent de globules graisseux et perdent la netteté de leur contour en se résolvant en une masse légérement granuleuse. Par la méthode de Benda, les globules graisseux sont brun noirâtre et la masse du plaste se traduit par de petits granules fuchsinophiles. Plus tard, les globules graisseux se fusionnent eux-mêmes en masses énormes graisseuses mais vertes par suite de la dissolution de la chlorophylle dans leur substance. Nous n'avons pas constaté, dans la parasitisme. ce dernier stade propre à la fanaison; une résorption intervient avant qu'il ne se produise.

Dans le cas de l'étude expérimentale que nous avons faite, on voit généralement les granulations huileuses apparaître presque instantanément dans toute la masse du chloroplaste (saccharose à 12. 5% et Ficaire) (Fig. 1). Les contours deviennent irréguliers. Aprés 5 à 10 minutes il y a fusion et lyse dans beaucoup de cellules. Au lieu de chloroplastes distincts, on a une masse uniforme verte et granuleuse, ou, parfois, des rubans à bords irréguliers, rappelant ceux du *Spirogyra,* par fusion latérale des grains verts. L'eau distillée a un effet bien différent, dans ce sens qu'elle ne fait pas apparaître de granulations huileuses. Les plastes, trés homogénes et transparents, subissent une lyse presque instantanée dans certaines cellules qui deviennent uniformément vertes. Dans les solutions de saponine, les chloroplastes s'étalent, émettent de fins prolongements en étoile qui deviennent coalescents d'un élément à l'autre, puis s'opére une fusion générale en une masse plus ou moins granuleuse avec gouttelettes d'huile. L'action est plus prompte dans les tissus envahis par le parasite que dans les tissus sains ("fragilisation plastidaire"). Nous avons également étudié l'action du chloroforme et de l'éther qui se raméne à celle d'un liquide déshydratant (hypertonique).

Une solution de lécithine à 1/1000 entraine aussi une fonte granuleuse, de même, une solution d'acide acétique à 1/20; l'action est trés rapide ce qui laisse concevoir quel trouble ce réactif peut entraîner quand on l'emploie dans certains fixateurs.

Le cas des chloroplastes de la pomme de terre atteinte "d'enroulement" présente un intéret trés particulier (Fig. 2). Sous l'influence de la fragilisation, résultant d'une hypotonie dont nous avons expliqué plus haut la cause, les chloroplastes cédent en quelques minutes à l'action de l'*eau ordinaire*; on peut assister, au moins dans les cellules lésées, où la pénétration du liquide se fait plus

Fig. 1. *Ficaria ranunculoides.* Parenchyme de la feuille.
Observation vitale de la dégénérescence des chloroplastes.

I, II, et III, en solution hypertonique (solution de saccharose à 12 pour 100 se concentrant par séjour de plusieurs heures sur la préparation.

IV, aspect rubanné par fusion latérale des chloroplastes.

V, à la solution de saccharose, on a ajouté 1 p. 100 de saponine. La figure montre le mode d'étalement des plastes en étoile, suivi de fusion avec dégénerescence granuleuse.

facilement, à la *vésiculisation* des chloroplastes. Nous n'avions pas encore rencontré ce phénoméne dans le cas des chloroplastes. Dans les diverses plantes étudiées par nous à ce point de vie, nous n'avions constaté que l'étalement de ces éléments prenant en même temps une consistance granuleuse. Au contraire, dans le cas de "l'enroulement," le chloroplaste so gonfle en bulle trés hyaline, sur ses bords se trouvent quelques granules incolores, tandis que le pigment vert se localise, à l'état de capuchon, sur un côté de la bulle. Plus tard, celles-ci élate, les granules se disséminent, le pigment devient lui-même épars, granuleux ou se résorbe.

Fig. 2. Pomme de terre fortement atteinte "d'enroulement". Cellule du parenchymle foliaire. Coupe fraiche montée dans l'eau ordinaire. On assiste, au bout de quelques minutes, á a vésiculisation des chloroplastes. Le pigment *p*, forme copuchon à la vesicule hyoline, sur le bord de celle-ci s'observent des granulations incolores *g*, provenant de la dégénérescence de la substance du plaste élaborateur.

En *A*, dégénérescence sans vésiculisation—En *B*, la cellule est rompue, l'eau a penètre plus facilement, la vésiculation s'est produite—En *C*, autre cas de vésiculisation—En *D* on voit divers aspects que peuvent prendre par dégénérescence sous l'action de l'eau ordinaire, les chloroplastes de la pomme de terre avec "enroulement."

B. Observations Apres Fixation et Coloration

Si, maintenant, au lieu d'observer directement sous le microscope, l'action de ces réactifs sur les tissus vivants, nous fixons ceux-ci et colorons aprés cette action, nous aurons des aspects que l'étude vitale préalable dont nous venons de rendre compte va nous permettre d'interpréter.

Nous avons surtout fait usage des fixations soit au formol (pur ou dilué), soit au bichromate-formol (méthode de Regaud) suivies de la coloration par l'hématoxyline ferrique (méthode de Heidenhain).

Avec la cellule saine, la méthode de Regaud donne des chloroplastes bien fixés ayant l'aspect à peu prés homogène; les mitaplastes apparaissent nettement dans les cas où ils existent (feuilles adultes de Ficaire ou de Seigle, par exemple) (Fig. 3); ils paraissent faire défaut, ou sont moins apparents, dans certains cas, la feuille de pomme de terre, par exemple. Le formal et même le bichromate-formol donnent des résultats trés particuliers dans certaines plantes. Ce fait

contribue à indiquer que les chloroplastes offrent des textures et compositions variables chez les espèces différentes de plantes.

Dans les feuilles de pomme de terre, par exemple, il se fait, sous l'influence du formol, tout un système d'alvéoles creusées dans la substance du chloroplaste; le fixateur de Regaud ne produit pas cet aspect au même degré[4]; si le même formol est appliqué à d'autres espèces de plantes: Ficaire, etc. etc., ces alvéoles n'existent pas ou sont à peine indiquées. Après fixation et coloration à l'hématoxyline ferrique, on peut assister, dans le cas de la pomme de terre, à un phénomène intéressant lors de la décoloration par l'alun de fer: lorsque celle-ci est assez poussée, le plaste (déformé comme nous l'avons dit par l'action du formol) n'est
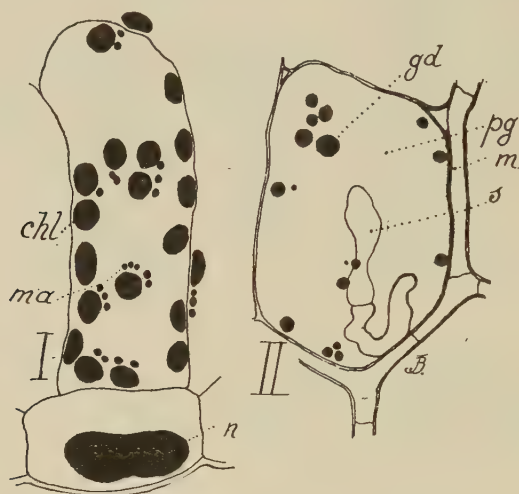
Fig. 3. *Puccinia dispersa* sur *Secale cereale*.—Fixation au bichromate-formol (méthode de Regaud), coloration à l'hématoxyline ferrique (méthode de Heidenhain).

I, Tissu non parasité. *chl*, chloroplaste; *ma*, mitaplastes; *n*, noyau. On voit une cellule de parenchyme en palissade et une cellule épidermique.

II, Une cellule parasitée, près du bord de la tache que produit le parasite. La différenciation en parenchymes palissadique et lacuneux n'est plus sensible. *m*, mycelium intercellulaire; *s*, suçoir; *gd*, globules de dégénérescence fortement colorables représentant ce qui subsiste des plastes et mitochondries (nous pensons qu'ils correspondent aux "nucléoles" du mycoplasme d'Eriksson). *pg*, cytoplasme finement granuleux.

bientôt plus représenté que par quelques globules colorés en noir (Fig. 4), résidus de la trame ou même, dans quelques cas, il y a persistance de globules contractés dans l'intérieur des alvéoles, globules qui étaient déjà visibles avant cette décoloration. Ce cas permet de se rendre compte que les granules ou globules, représentant tout le plastidome après dégénérescence, proviennent bien de la substance du plaste formateur; par exemple, dans le cas des chloroplastes, ils répondent à la substance du plaste et non au pigment élaboré par lui. Le pig-

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[4] Nous devons signaler que le matériel conservé dont nous nous sommes servi était fortement atteint de taches blanches de "mosaïque." Nous allons reprendre l'étude de ce cas particulier avec des matériaux frais.

ment cholorphyllien subit, en effet, une dégénérescence huileuse, or les globules huileux n'apparaissent pas par la méthode de Regaud et coloration à l'hématoxyline ferrique; ils se montrent, au contraire, par la fixation chromo-osmique de la méthode de Benda, par la fixation au Flemming, etc.

Fig. 4. Pomme de terre. Feuille (avec mosaïque). Formol et Hématoxyline ferrique.

Les choloroplastes présentent les alvéoles caractéristiques de la fixation au formol dans le cas de cette plante (elle se produit aussi plus ou moins par la méthode de Regaud).

La décoloration plus ou moins grande fait apparaître de faux nucléoles. d, Portions décolorées du chloroplaste; m, portions restées colorées.

En B on remarque des globules trés chromophiles souvent inclus dans les alvéoles produites par la fixation.

Résumé Des Caractéres Morphologiques de la Dégénérescence Des Chloroplastes

Ce que nous venons d'exposer permet de résumer les caractéres morphologiques de la dégénérescence des chloroplastes.

Elle résulte, le plus souvent, d'actions entraînant des pertubations de la pression osmotique intra cellulaire; le parasitisme a comme effet le plus général d'entrainer des troubles de cette nature. Il se produit:

1. Une dégénérescence huileuse du pigment aboutissant à la formation de granules colorables à l'acide osmique (méthode de Benda, Flemming), mais non par la méthode Regaud-Heidenhain;

2. Une dégénérescence granuleuse de la substance du plaste support du pigment, aboutissant, comme dans de cas des mitochondries et des autres plastes, à la

formation d'un résidu formé de quelques éléments globuleux fortement sidéro-
philes et apparaissant, par conséquent, colorés en noir foncé par l'hématoxyline
ferrique succédant à la fixation au formol ou au bichromate-formol. Ces glo-
bules (de nature albuminoîde, lipoîdique, etc.) correspondent, pensons nous,
aux "nucléoles" du mycoplasme d'Eriksson.

3. Quelquefois (nous ne l'avons encore constaté que dans les feuilles de pomme
de terre atteinte d'"enroulement"), on peut observer le gonflement du chloro-
plaste en une bulle hyaline (par la simple action de l'eau ordinaire dans le cas
que nous venons de mentionner). Le pigment forme capuchon sur une faible
partie de la surface, tandis que quelques granules incolores se voient à la péri-
phérie de la bulle. Aprés disparition de celle-ci les granules de dispersent pour
se fusionner ensuite; on perd la trace du pigment. Quoi qu'il en soit, les méthodes
mitochondriales traduiront toujours ces faits par la coloration d'un certain
nombre de globules plus ou moins volumineux.

<center>CRITIQUE DES BASES CYTOLOGIQUES DE LA
THEORIE DU MYCOPLASMA</center>

En conséquence, nous pensons qu'Eriksson a décrit comme "nucléoles" de
son "mycoplasme" de simples états de dégénérescence du chondriome-plastidome
donnant un magma granuleux avec des globules trés colorables correspondant
au résidu de ces éléments. Ce sont ces globules qui correspondraient aux "nucléo-
les." On sait que ces derniers constituent toute la base de la théorie du myco-
plasme au point de vue cytologique.

Les globules dont on constate la présence dans les préparations fixées et
colorées peuvent correspondre soit à la dégénérescence de la substance fonda-
mentale des plastes, soit à celle des pigments élaborés par eux, soit aux deux,
suivant la méthode d'observation mise en œuvre.

La dégénérescence elle-même résulte soit: (1) de l'action du parasite déjà
présent sous sa forme ordinaire et d'origine externe (par opposition à l'origine
interne qu'implique la théorie du mycoplasme dans le cas d'une invasion prim-
aire); (2) plus souvent d'une fragilisation du chondriome-plastidome, consé-
cutive à la présence du parasite, que le fixateur traduit brusquement en une
dégénérescence granuleuse. Notons, en effet, qu'Eriksson ne signale ses "nucléo-
les" que sur préparations fixées et non sur préparations vivantes et qu'il n'a pas
employé les méthodes mitochondriales mettant particuliérement à l'abri d'une
altération cyto-structurale imputable au fixateur seul.

La persistance des mitaplastes aprés la destruction des chloroplastes peut
expliquer aussi les "nucléoles" du mycoplasme.

Il est enfin une troisiéme cause de confusion que nous avons signalée il y a
déjà longtemps[5] mais qui est certainement moins importante que les précédentes:
nous voulons parler de la dégénérescence non plus du contenu de la cellule hôte,
mais bien de suçoirs intra cellulaires du champignon de la rouille dans certaines

[5] L'hypothése du mycoplasma et les corpuscules métachromatiques. Compt. Rend. de l'Acad.
des Sci., 6 mars, 1911; Beauverie, J. La signification des corpuscules métachromatiques dans les
cellules des céréales infestées par la rouille. Comp. Rend. Soc. de Biologie, 25 mars, 1911.

cellules de la périphérie des taches. Cela se produit là où précisément le myco-plasme s'organiserait en mycelium. Nous avons interprété cette désorganisation comme une sorte de phagocytose sur place. Les corpuscules de métachromatine—dont nous avons souvent signalé la résistance aux actions parasitaires—persistent. Ils apparaissent alors en bleu sombre ou en rouge (métachromasie) sur les pré-parations fixées par la plupart des fixateurs et colorées par une couleur bleue d'a-niline. Par contre, ils ne sont généralement pas apparents par la coloration avec l'hématoxyline ferrique.

Les granulations qui ponctuent le magma protoplasmique sont donc d'origines trés différentes suivant le mode d'observation que l'on adopte, mais elles peuvent simuler également les nucléoles d'un mycoplasma (voir Fig. 3).

On sait que M. Eriksson, qui a créé son hypothése à propos des rouilles des céréales, et autres Graminées (1900), l'apostérieurement étendue à beaucoup d'autres maladies,[6] notamment: la rouille des mauves (1911), le mildiou de la pomme de terre (1899 et 1916), celui de l'épinard (1918), etc. Il a décrit deux phases dans la manifestation du mycoplasme: 1e une fonte chlorophyllienne, 2e l'apparition des nucléoles. Nous venons de montrer comment nous intérpré-tons cette succession comme deux phases de la dégénérescence du contenu cel-lulaire.

Cette question du mycoplasme sommeillait depuis quelques années, mais elle reprend une actualité nouvelle: Eriksson lui a donné lui-même une plus grande extension; Löhnis et son école prétendent que les bactéries présenteraient au cours de leur évolution un état "symplastique" qui nous parait présenter une grande analogie avec le mycoplasme. Ils procédent peut être d'une même il-lusion.[7] On soutient aujourd'hui que des bactéries, telles que le bacille de la tuberculose, peuvent prendre des formes filtrantes; on n'est pas assuré encore que le *Bacillus tumefaciens* de la *Crown gall* ne revête pas dans la tumeur une forme invisible. Toutes ces questions sont connexes, aussi croyions nous qu'il n'était pas inutile de reprendre les faits cytologiques sur quoi on étaye la théorie du Mycoplasme.

LES MITAPLASTES

Les mitochondries non plastogénes ("inactives" de Guilliermond) se sont montrées plus résistantes que les plastes et chloroplastes aux actions fragilisantes ou destructrices des parasites ou des agents physiques. On peut le vérifier, par exemple, avec la Ficaire parasitée par *Uromyces Ficariae* traitée par la sapon-

[6] Voir la liste de ces maladies in: Eriksson. La théorie du mycoplasme, sa portée scientifique et sa perspective pratique. Bull. des renseignements agricoles **13**: mars, 1922.

Les microphotographies des "stades nucléolaires" que nous avons sous les yeux dans ce mémoire et dans les deux suivants ne nous laissent pas de doute que le seul argument cytologique par lequel Eriksson a pensé étayer sa théorie, repose sur une interprétation erronée de la structure cellulaire dans l'état pathologique.

Eriksson, J. Développment primaire du Mildiou (Phytophthora infestans) au cours de la végétation de la pomme de terre. Rev. gén. de Botanique **29**: p. 257 et suiv. *pl. 4 à 15.* 1917; Eriksson, J. Zur Entwickelungsgeschichte des Spinatschimmels (Peronospora Spinaciae)—Arkiv för Botanik **15**: 25 p. *4 pl.* 1918.

[7] Beauverie, J. Le symplasme bactérien existe-t-il? Compt. Rend. Acad. des Sci., 1925.

ine, etc.). Sur une préparation ainsi traitée, puis fixée par la méthode de Regaud et colorée par l'hématoxyline ferrique, elles apparaissent encore sous leur forme habituelle (granules souvent en chapelet dans la Ficaire) alors que le plastidome a déjà subi une fonte caractérisée et n'apparait plus que sous la forme de rares et plus ou moins volumineux globules trés chromophiles.

Dans la Mauve parasitée par *Puccinia malvacearum*, ces mitaplastes paraissent plus nombreux dans les cellules de la périphérie des taches que dans les parties saines. Nous les avons vus encore particuliérement abondants dans les feuilles du Seigle attaqué par *Puccinia dispersa*.

Rôle Des Membranes Cellulaires

On remarque une assez grande irrégularité de cellule à cellule dans les modifications cyto-structurales qui se produisent sous l'action de réactifs ou de parasites. Il s'agit généralement d'un retard. Il n'est pas douteux que l'explication de ce phénoméne soit à rechercher dans les propriétés spéciales des membranes cellulosiques et protoplasmiques qui par leurs particularités de constitution peuvent influencer différemment les phénoménes osmotiques.

Deux Grandes Categories D'effets Biologiques D'un Parasite Sur Son Hôte

Il faut nettement distinguer, au point de vue de l'etude cytologique: (1) le cas où l'action du parasite entraîne un affaiblissement de vitalité auquel peut même succéder la mort, et celui (2) où il produit, au contraire, une excitation spéciale engendrant des morphoses. C'est le premier cas seulement que nous avons considéré dans le présent travail.

"Hypersensibilite" et "Sensibilite" Aux Rouilles Des Hôtes Cereales

Les phénoménes suivants se produiraient: Dans le cas des espéces ou variétés "hypersensibles" à la rouille, dés la pénétration du mycelium germinatif dans les premiéres cellules au delà de l'ostiole, il y a destruction des mitoplastes ce qui engendre des produits de dégénérescence: huiles, substances albuminoîdes, lipoides, etc., l'architecture colloidale du complexe cytoplasme-noyau est également détruite, la cellule est tuée. Le champignon ne pouvant vivre en saprophyte, ne s'étend pas plus loin. C'est la mort par inanition dont l'hypothése a été émise depuis longtemps par M. Ward. Il se produit des taches d'hypersensibilité (décoloration par disparition des chloroplastes) mais pas de fructifications.

Dans le cas des espéces ou variétés simplement "sensibles," le mycelium fragilise et détruit la plupart des mitoplastes et plastes, mais en laissant au complexe noyau-cytoplasme une certaine vitalité. Le champignon exerce toujours sa qualité de parasite tout en rendant disponibles les produits nécessaires à son alimentation.

Reconstitution Schématique Des Effets De L'Attaque D'un Parasite Sur la Structure Cellulaire

On peut concevoir schématiquement, et d'une façon pour ainsi dire cinémato-
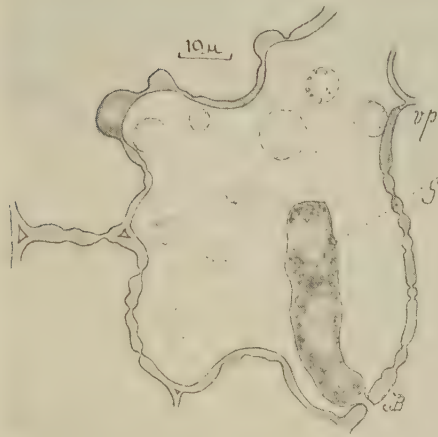
Fig. 5. *Aecidium Pulmonariae* sur feuille de *Pulmonaria longifolia*. Une cellule de l'épiderme recouvrant une tache d'*Aecidium*. Observation sur le vivant dans une solution de saccharose 12%, aprés 2 heures de séjour dans le liquide (légére hypertonie). Il s'est produit aux dépens des plastes des vésicules trés hyalines et distinctes surtout par la présence de granulations ponctiformes. Dans la cellule, on remarque la présence d'un suçoir de la rouille. Ce phénoméne de vésiculation, s'il n'est causé directement par le parasite, est favorisé par lui (fragilisation plastidaire).

Fig. 6. *Uromyces Ficariae* attaquant *Ficaria ranunculoides*. Observation vitale. En *C* les chloroplastes fragilisés sous l'action du parasite dont on voit le mycelium intercellulaire *m*, subissent un début de dégénérescence granuleuse. En *B*, une cellule dans laquelle pénétre un suçoir; les chloroplastes ont été résorbés aprés dégénérescence. En *A*, les chloroplastes ont échappé a toute action nocive (effet de la membrane cellulaire).

graphique, l'action d'un parasite sur la structure cellulaire. L'action du champignon peut être directe (mycelium intra cellulaire ou suçoirs) ou indirecte (mycelium intercellulaire). Sous cette action, certaines mitochondries et des plastes se transforment en vésicules avec granules périphériques (Fig. 5); ils éclatent (à la façon d'une bulle de savon, si l'on veut, laissant un résidu granuleux quelquefois trés reduit, mais engendrant par leur fusion des globules peu nombreux et assez volumineux. D'autres plastes, notamment des chloroplastes, sans se vésiculiser, perdent la netteté de leur contour, s'étalent en subissant une fonte granuleuse (Fig. 6): substances huileuses pour les pigments xantho- ou chlorophylliens et matiéres albuminoîdes pour la substance fondamentale du plaste), leurs masses se fusionnent parfois en une seule remplissant plus ou moins complétement la cellule. Cette fonte peut être appelée "chondriolyse." Ultérieurement, ces masses se résoberont plus ou moins complétement et la cellule pourra apparaître vide de tout contenu.[8]

Dans quelques cas, paraissant plus rares, le chloroplaste subit une vésiculisation analogue à celle que nous mentionnons au début de ce paragraphe: le plaste devient une vésicule hyaline avec granules périphériques et le pigment forme capuchon; puis tout se résoud en quelques granulations qui peuvent se fusionner (elles sont trés colorables).

Ce tableau résulte de l'observation de faits experimentaux. Quant à l'observation directe, *in vivo*, de l'action du parasite, elle ne saurait permettre que bien rarement la constatation de la vésiculation par exemple. Ce sont là, en effet, des états extrêmement instables, traduisant un défaut d'équilibre incompatible avec la permanence. Ils ne sauraient être que transitoires ou même instantanés dans la plante vivante. Nous reprendrons volontiers, à ce propos, la comparaison de la "bulle de savon," car elle fait image.

APPLICATION DE LA THÉORIE DE LA RESISTANCE PLASTIDAIRE A L'APPRECIATION DE LA RESISTANCE AUX MALADIES

Lorsque la généralité de cette théorie sera vérifiée, elle parait à même d'apporter un élément d'appréciation de la sensibilité ou résistance plus ou moins grande d'une espèce, variété, lignée ou hybride, vis à vis d'un parasite.

RÉSUMÉ

Nous avons considéré dans ce travail les principaux points suivants: Variations de la résistance des mitochondries et plastes aux actions osmotiques, leur fragilisation sous l'influence d'un parasite. En derniére analyse, l'action de celui-ci se traduit dans la cellule par une modification de la tension osmotique: Description des phénoménes morphologiques de la dégénérescence des mitochondries et des plastes sous l'action de certains réactifs physico-chimiques et celle des parasites. Nos conclusions concernant le mécanisme de l'action du parasite sur l'architecture cyto-structurale résulte de l'observation directe et plus encore, de l'étude expérimentale de l'action des réactifs en question.

[8] Nous laissons de coté le noyau, déja étudié à ce point de vue.

Comparaison de ces phénoménes observés sur préparations vivantes d' une part, et sur préparations fixées et colorées d'autre part. Interprétation des faits morphologiques que l'on observe dans ces derniéres conditions.

Esquisse des modifications qui paraissent devoir se succéder dans la cellule lorsque celle-ci est attaquée par un parasite champignon: son action se traduit par la création d'un état hypertonique, la mort du protoplasma qui devient finement granuleux. L'invasion de l'eau, qui survient alors, améne la transformation des mitochondries et de certains plastes en vésicules qui éclatent en laîssant subsister quelques granules. Ils se fusionnent plus ou moins. Les chloroplastes subissent une fonte granuleuse: goutelettes d'huile résultant du pigment et globules provenant du substratun albuminoîde ou lipoîde du plaste. Ces granules se fusionnent en globules plus ou moins volumineux mais peu nombreux. Ces produits de dégénérescence peuvent être bientot résorbés plus ou moins complétement.

Dans le cas de la maladie de "l'enroulement" de la pomme de terre, la fragilisation trés grande des chloroplastes résulte peut-être d'une hypotonie consécutive à la condensation des sucres *in situ* dans les feuilles, en amidon; ils cédent à l'action de l'eau ordinaire.

Les préparations fixées et colorées, font souvent apparaître des granules plus ou moins volumineux, trés chromophiles, représentant un résidu des granules fusionnés de dégénérescence dont nous venons de parler. Les globules que l'on met ainsi en évidence ne sont pas forcément de même origine suivant les diverses méthodes de fixation-coloration employées.

Nous faisons l'application de ces données à la critique des bases cytologiques de la théorie du "mycoplasme." Nous concluons que les "nucléoles" d'Eriksson répondent à une interprétation erronée des faits de dégénérescence du chondriome-plastidome. Ils ne seraient autres que les globules résiduaires qui proviennent de celle-ci. Cette dégénérescence elle-même, résulte, soit de l'action directe du mycelium, soit de l'action de certains fixateurs agissant sur ces éléments figurés de la cellule, préalablement "fragilisés" par le parasite.

On obtient plus ou moins facilement la dégénérescence des plastes par la méthode expérimentale, suivant qu'ils se trouvent plus ou moins "fragilisés" par une action parasitaire: c'est ainsi que les chloroplastes des feuilles de la pomme de terre atteinte "d'enroulement" cédent trés vite au simple contact de l'eau ordinaire.

Nous faisons l'application des données précédentes à l'explication de la théorie de Marshall Ward concernant "l'hypersensibilité" et la "sensibilité" des Céréales aux rouilles.

Nous indiquons l'application possible de la théorie de la fragilisation plastidaire et mitochondriale à l'étude et au choix des espéces, variétés, lignées, hybrides, résistants aux maladies cryptogamiques.[9]

[9] Beauverie, J. Quelques aspects de la dégénérescence des plastes. Rev. gén. de Bot. **40**; 1928.

PHYSIOLOGIC SPECIALIZATION IN PATHOGENIC FUNGI[1]

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INTRODUCTION

Since Schroeter (71) in 1879 first suggested that there was physiologic specialization in fungi, the phenomenon has been widely investigated. The classic researches of Eriksson (31), Carleton (23), Neger (62), Marchal (60), Ward (87), Salmon (68, 69), Klebahn (48), Freeman and Johnson (36), Reed (64), and others have been summarized before and are too well known to require extensive review here.[3]

The work of these investigators, as well as that of many others, has shown that there is physiologic specialization in many groups of pathogenic fungi: the rusts (31, 36, 78, 59); the smuts (65, 33, 74); the powdery mildews (60, 62, 64,); *Septoria* (8); *Helminthosporium sativum* (24); *H. gramineum* (45); *Colletotrichum lindemuthianum* (6, 30, 52); *Claviceps purpurea* (73); *Fusarium spp.* (16, 90); *Sclerotinia spp.* (89, 32, 72); *Pestalozzia guepini* (50); *Rhizopus nigricans* (39); *Rhizoctonia* (66, 61, 14); *Phytophthora* (53); and others too numerous to mention. In fact, the statement sometimes is made that all species of pathogenic fungi comprise many physiologic forms. Just how accurate this statement is I am not prepared to say. It certainly is true, however, that *Colletotrichum lindemuthianum* long ago ceased to be merely *C. lindemuthianum*: it has become *C. lindemuthianum*, strains alpha, beta, and so on (6, 22); *Puccinia graminis* long ago ceased to be merely *Puccinia graminis*: it first became *P. graminis tritici*, *P. graminis secalis*, etc. Now it has even become *P. graminis tritici*, physiologic

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forms 1 to about 50 inclusive (76).[4] And *Puccinia triticina* once was *P. rubigo vera*, then it became *P. rubigo-vera tritici*, and, if the same terminology had been retained, it would now be *P. rubigo-vera tritici*, forms 1 to at least 12, inclusive (59). More categories! To be sure; but categories based primarily on behavior, not morphology. And it is this behavior which pathologists must know, complex though it often is.

Physiologic specialization undoubtedly assumes its greatest importance in epidemiology studies, in quarantines, and in the development of disease-resistant varieties of crop plants. A thorough study of physiologic specialization must become routine work in investigations on the pathogenicity of fungi. It is prerequisite to surest and most rapid progress. Therefore it is essential to take stock of our present knowledge of the phenomenon.

How Can Physiologic Forms be Recognized?

The concept of physiologic specialization has changed somewhat in recent years. Formerly it was supposed, and we still often fall into the error of thinking, that forms differ from each other only in their effect on host plants. However, this is not true. It is quite true that physiologic forms of certain apparently obligate parasites, like the rust fungi and the powdery mildews, can be differentiated readily only by their action on certain differential host plants. But there also are other methods. Forms can be recognized 1, by their pathogenic effect on host plants; 2, by morphology, to a limited extent; 3, by cultural characters on artificial media; and 4, by physico-chemical reactions.

It hardly seems necessary to discuss methods of distinguishing physiologic forms by their parasitic behavior. One simply inoculates certain species or varieties of plants with cultures of the same organism from different sources and then observes the results. If the different cultures consistently produce different pathological effects, they are obviously different pathogenically and are properly designated as physiologic forms, provided they are not very dissimilar morphologically. There may even be different categories of physiologic forms. *Puccinia graminis* furnishes a good example.

Two categories of parasitic strains have been recognized in *P. graminis*: varieties and physiologic forms. Formerly the varieties were called biologic forms, biologic races, physiologic forms, physiologic species, biologic species, physiologic races, racial strains, parasitic strains, and even specialized varieties. Previous to 1916 only one category of parasitic strains was known within the species *Puccinia graminis*. These were most commonly called biologic forms. The following were recognized in the United States: *Puccinia graminis tritici*, *P. graminis secalis*, *P. graminis avenae*, *P. graminis phleipratensis*, *P. graminis agrostis*, and, more recently, *P. graminis poae*. They were distinguished from each other principally by differences in their pathogenicity on plants belonging to different genera, but since 1916 it has been found that *P. graminis tritici* actually comprises many parasitic strains which differ in their effect on varieties of *Triticum* spp. In the same way, it has been found that *P. graminis avenae* and

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[4] Unpublished data included here.

P. graminis secalis comprise several parasitic strains, which differ from each other in their effect on varieties of *Avena spp.* and *Secale cereale* respectively. That is, there are biologic forms within biologic forms. Inasmuch as *Puccinia graminis tritici, P. graminis avenae,* and the other parasitic strains having Latin names differ from each other somewhat morphologically, they have been designated as varieties and their component strains as physiologic forms. *Puccinia graminis tritici,* therefore, is a variety, and *P. graminis tritici 17* is a physiologic form. For instance, *Puccinia graminis tritici 17* means physiologic form 17 of the variety *tritici* of the species *P. graminis.* Table 1 may make the matter clearer.

TABLE 1. Varieties of *Puccinia graminis* in the United States with the principal host plants for each, also physiologic specialization within the varieties

Variety	Host plants[a]	Physiologic forms
tritici	Wheat, Barley, Rye[c], Agropyron spp.[b] (A. repens, very resistant), Bromus spp., Elymus spp., Hordeum spp., Hystrix spp.	More than 50, differing in their effect on varieties of Triticum spp.
secalis	Rye, Barley, and same grasses as above. (Agropyron repens very susceptible).	About a dozen, differing in their effect on varieties of rye.
avenae	Oats, Agrostis exarata, Alopecurus spp., Anthoxanthum spp., Arrhenatherum elatius, Bromus tectorum, Calamagrostis canadensis, Dactylis glomerata, Holcus lanatus, Koeleria cristata, Panicularia pauciflora, Phalaris spp.	Five or six, differing in their effect on varieties of oats.
phleipratensis	Timothy, Oats[c], Barley[c], Alopecurus spp., Dactylis glomerata, Festuca spp., Holcus lanatus, Koeleria cristata.	None demonstrated.
agrostis	Agrostis spp. and grasses listed under phleipratensis, except Festuca spp.	do
poae	Poa spp.	do

[a] Achyrodes is fairly susceptible to all varieties.
[b] Where several species are indicated, it does not follow that all species of the genus are susceptible; where only one species is indicated, it does not necessarily mean that other species may not be susceptible.
[c] Infection usually weak.

Are the so-called varieties of *Puccinia graminis* true morphological varieties? Yes and no. Some of them differ from each other so much in the morphology of urediniospores that it is quite proper to consider them as varieties. But the observed morphological differences between others are neither great nor consistent enough to enable one to distinguish between them readily on this basis. The most characteristic differences between the varieties is their parasitic behavior. What, then, is the justification for calling them varieties? It is very largely a matter of convenience. And, if further justification is necessary, one can always fall back on the argument that there are some morphologic differences between them.

One of the most remarkable things about the varieties and physiologic forms of *P. graminis* is the absolute certainty with which they can be determined by

their pathogenicity on selected host plants. Levine and I have identified certain forms obtained from three different continents, and their effect on host plants was exactly the same, regardless of their origin. While the development of all varieties or physiologic forms on host plants is influenced by environmental conditions, the constancy in pathogenicity is quite remarkable. There has been an impression on the part of some pathologists that physiologic forms are rather vacillating entities, if indeed they are entities at all. But it is far easier and far more satisfactory to distinguish between physiologic forms of *P. graminis tritici* by their effects on differential hosts than it is to distinguish between many closely related species of fungi by their morphology, and I am confident that the determination of physiologic forms by their effect on host plants often is more precise and accurate than the determination of morphologic species.

Morphology, while not always an adequate criterion of identity, often is a valuable aid in the recognition of forms. As previously mentioned, some of the "major physiologic forms," or so-called varieties, of *P. graminis* can be distinguished from each other quite readily on the basis of size, shape, and color of the urediniospores. The *tritici* and *agrostis* varieties can be distinguished from each other as readily as can many well-established species of fungi, although others, such as the *secalis* and *avenae* varieties, cannot be differentiated from each other so easily (75, 55). It is possible, also, to demonstrate considerable and consistent differences between the physiologic forms of *P. graminis tritici* (56), *P. graminis avenae* (3), etc. These differences are sometimes fairly large. However, in making comparisons, it is necessary to measure spores produced under exactly the same conditions in order to get comparable results (75, 55). While morphology may help, therefore, in determining physiologic forms, its usefulness is limited.

If physiologic forms are morphologically distinct, why not call them species? For several reasons: first, because the differences between them are primarily physiological and not morphological; second, because it is impossible to distinguish between some of the forms unless a large number of spores is measured; and, third, because the morphology of some forms varies so greatly as to make it impracticable to identify them in this way.

It certainly is possible to distinguish between many physiologic forms on the basis of cultural characters on artificial media. At Minnesota, we have recognized physiologic forms of *Claviceps purpurea*, *Helminthosporium sativum*, *Brachysporium sp.*, *Polyspora lini*, *Sclerotinia americana*, *Colletotrichum lindemuthianum*, *Fusarium lini*, *F. graminearum*, *F. moniliforme*, *Ustilago zeae*, *U. tritici*, *U. nuda*, and *Sorosporium reilianum* by cultural differences. In some cases the differences are so distinct that one would be inclined to consider the different forms as species. However, there may be great variation on different media. Different physiologic forms of *H. sativum*, for instance, may look almost exactly alike on one culture medium, but on another they may be entirely different. And cultures of the same form on different media may look like several different species.

Whether cultural characters ever will enable pathologists to know forms

sufficiently well for pathologic purposes remains to be seen. Can the cultural test be substituted for the pathogenicity test? It would obviously be an easy method of determining physiologic forms if one could merely grow them in culture on standardized media and know from that how they would behave pathogenically. This may be possible to a limited extent, but it is doubtful whether this method ever will replace the pathogenicity test. Cultural characteristics, however, certainly will often enable pathologists to obtain the first definite indication of physiologic specialization. This already has been true of *Helminthosporium sativum* (24, 25) *Fusarium lini* (16), *Ustilago zeae* (74), and many others.

As would naturally be supposed, physiologic forms often differ also in their physico-chemical reactions. The very term "physiologic form" implies this difference. These differences long have been recognized in working with bacteria. Many so-called species of bacteria are in reality nothing but physiologic forms. This seems to be true of the group of organisms causing soft rot of vegetables and consisting of such species as *Bacillus carotovorus*, *B. atrosepticus*, etc. Unpublished studies made by Leach at Minnesota strongly indicate the correctness of this assumption. It is the conventional procedure to differentiate species of bacteria on the basis of physiological behavior. This has not been done to so great an extent with fungi, but there are similar differences between strains. The work of Dox (27), and of several other investigators, has shown clearly that fungi may look alike but be quite different in their fermentative capabilities. Not only that, but it has been shown that these differences, for the most part, are inherent and inherited. Recently it has been shown by Letcher and Willaman (54) that physiologic forms of *Fusarium lini*, which are detected primarily by cultural characters and pathogenicity, also differ considerably in their ability to produce alcohol from sugars. In fact, there seems to be a fairly close correlation between virulence and ability to produce alcohol.

Different forms also may have quite diverse temperature requirements. Edgerton (29) showed that forms of *Glomerella* differed distinctly in this respect. Weimer and Harter (88) and Harter and Weimer (39) have shown that there are similar differences between species of *Rhizopus*, and they found one strain of *R. nigricans* which had a lower optimum than 17 others which they studied. Hursh (43) has shown that different physiologic forms of *P. graminis tritici* have different optimum temperature requirements. Johnson (45) has shown that there are at least two strains of *Helminthosporium gramineum* which differ in their reaction to temperature. One of the strains with which he worked had a rather low optimum temperature, while that of the other was much higher. It is obvious that this may have considerable effect on the pathogenicity of the organism. Early-sown barley usually is more subject to stripe than that which is sown later, because of the low optimum temperature for at least some strains of the organism. The condition, however, easily might be reversed if the form with a higher optimum temperature happened to predominate in a given region.

There are, then, four general methods of recognizing physiologic forms: pathogenicity; morphology, to a limited extent; cultural characters; and physico-chemical relations. Entities, within a species, which differ from each other

primarily and consistently physiologically should be considered as physiologic forms, whether the differences are in pathogenicity or other physiologic attributes.

THE ORIGIN AND CONSTANCY OF PHYSIOLOGIC FORMS

What is the origin of physiologic forms? This question is not essentially different from the age-old question of the origin of species. But the important practical question which pathologists must answer is: how stable are the forms? The answer apparently is that they often are as stable as species themselves. Many mycologists apparently still cling to the idea that physiologic forms are less stable than morphologic species, apparently forgetting that genetic factors determine physiologic behavior as well as morphology. It often has been assumed that physiologic characters are more easily changed than morphologic ones. But are they?

Three explanations usually are offered for the origin of physiologic forms: adaptation, or so-called education; hybridization; and mutation.

For many years, following the remarkable results obtained by Ward (87), Salmon (69), Pole-Evans(63), Freeman (35), and Freeman and Johnson (36), it was generally supposed that the pathogenicity of physiologic forms could be changed easily by host influence. It was stated that if a form of rust, for instance, were transferred several successive times to a resistant host, it gradually acquired the ability to attack the host normally. And these investigators also thought that certain plants could act as "bridging hosts." For example, Ward (87) explained bridging with respect to *Puccinia dispersa* on *Bromus spp.* as follows: The rust from species A could not infect species C, but it could infect species B, intermediate taxonomically between A and C. On B the rust acquired the ability to infect C, and B therefore served as a "bridge" between A and C.

The theories of adaptation and "bridging hosts" were, and sometimes still are, accepted as facts. Extensive investigations, however, indicate that physiologic forms, of many fungi at least, do not gradually adapt themselves to new hosts. Neither has it been possible in later years to substantiate the results of earlier investigators on bridging hosts. The work of Stakman, Parker and Piemeisel (77) and Stakman, Piemeisel, and Levine (79) on the rusts indicates that physiologic forms, in these fungi at least, do not change their pathogenicity readily as a result of host influences. In fact, Piemeisel, Levine and I never have been able to detect the faintest evidence of bridging nor of a gradual adaptation of forms of *P. graminis* to new hosts.

The investigations of Thom (81) on the cultural characters of *Penicillium spp.* and of Dox (27) on the fermentative abilities of different strains of *Penicillium* also indicate rather clearly that physiologic forms do not easily and permanently change their physiologic characteristics to adapt themselves to new environmental conditions.

Most of the evidence at present seems to be that physiologic characters in pathogenic fungi are at least as stable as morphologic characters. They are due to genetic factors, the expression of which may be influenced to a considerable

extent by environment; but there is no strong evidence that they can be changed by environment. But the idea of adaptation and bridging still is widely held and cannot be dismissed arbitrarily.

Recently Hammarlund (37) has repeated some of Salmon's work with the powdery mildews. He was able to confirm part but not all of it. It will be remembered that Salmon (69, p. 107) obtained results from which he concluded that "the restriction in power of infection characteristic of biologic forms breaks down if the vitality of the leaf on which the conidia are sown is interfered with in certain ways." For instance, *Erysiphe graminis* from *Hordeum sylvaticum* could not infect normal wheat leaves, but it did infect injured wheat, on which it then acquired the ability to infect uninjured plants of the same variety. Hammarlund made similar experiments and states that *E. graminis tritici* consistently infected injured barley, but did not thus acquire the ability to attack uninjured barley plants.

Levine and I have tried to confirm Hammarlund's results but have been unable to do so. Attempts were made to infect several varieties of barley with *Erysiphe graminis tritici*. The plants were injured in the approved manner and then inoculated. Every conceivable form of torture was applied to them; but, although some two thousand plants of barley, rye, and oats were subjected to inoculation, all of them refused to take the mildew.

There must be some explanation for these discrepancies in results. Is the technic faulty on one or the other side of the Atlantic; does the European *E. graminis* change more easily than that in the United States; or do different varieties of wheat and barley react entirely differently to the mildew? Whatever the explanation, it cannot be laid down as a general rule that the infective capacity of physiologic forms of *E. graminis* can be changed at will by making them consort with certain real or theoretical host plants.

Do physiologic forms of pathogenic fungi hybridize? There is no reason why they should not; it would be strange if they did not. Saito and Naganishi (67) and Blakeslee (9) long ago showed that there were different sexual strains of the Mucorales and that they could hybridize. The more recent work of Kniep (49), Buller (18), Hanna (38), and others also is very suggestive in this respect. Is there any reason why different physiologic forms of rust fungi, for instance, may not hybridize in the aecial stage? It seems almost a foregone conclusion that they sometimes do, but I know of no case in which it has been conclusively demonstrated. Levine and I have obtained circumstantial evidence that different forms of *P. graminis* hybridized on the barberry, and produce new forms, but we could not prove it conclusively with our material.

Pathogenic fungi apparently mutate, some of them very rapidly and frequently, others more rarely or possibly not at all. Here again pathogenic fungi do not seem to be a law unto themselves but seem to be governed by the duly constituted laws of heredity. Blakeslee (10), Burger (20), Brierley (11, 12, 13), Stevens (80), La Rue (51), Christensen (25), Leonian (53), Brown (17), and others studied mutation, although they may not all agree in calling the phenomenon by this name. Christensen and Brown both were able to influence the

frequency of mutations by altering cultural conditions. One of the commonest forms of mutation is the production of sectors in cultures; very often there seems to be the loss of a factor for color. Whether these sectors constitute true mutation may be open to question. However, if what we seem to know about sexuality and nuclear phenomena in fungi actually is true, then there seems no valid reason why we should not consider cultures of fungi asexually propagated from single asexually produced spores as clonal lines. The mycelium of these clones may be heterozygous, as is often the case in clones of higher plants. But this should not affect the case. Sectors, different from the parent colonies, appear. And, when they retain their characters in subsequent generations, why are they not comparable with somatic or bud mutations? Possibly these new entities may be segregates of unobserved natural crosses which occurred unobserved in the past, although that seems improbable in many cases. Whatever they are, they often appear suddenly, differ profoundly from the parent colonies, and apparently are not due to a normal process of segregation and recombination. For the present, therefore, we may be justified in calling them mutants.

The mutation of pathogenic fungi is interesting enough as a biological phenomenon, but the vital question for the pathologist is: is there a change in pathogenicity corresponding with the change in appearance? Sometimes there is. Christensen (25) found that some mutants of *Helminthosporium sativum* behaved quite like their parents, others were less virulent on host plants, and still others were much more virulent than their parents. Recently Christensen and I have studied a similar phenomenon in *Ustilago zeae*. Numerous sectors occurred in cultures of some physiologic forms of this fungus. A striking case of loss of virulence was encountered in studying a form from Pennsylvania. The parent colony was purplish on many media and was the most virulent of about a dozen forms whose pathogenicity was studied. The sector was white to tan in color and was extremely weak pathogenically. The parent colony produced very large smut galls on virtually all parts of the inoculated plants of certain selfed lines of corn, while the sector produced very small ones or none at all. Mutants, therefore, often are less virulent than their parents, but it is highly significant that they sometimes are more virulent pathogens in the making.

As far as I am aware, it has never been demonstrated that the rusts or powdery mildews mutate. As a matter of fact, one obtains the impression of remarkable fixity when working with these fungi. We have cultured one form of *P. graminis tritici* continuously in the greenhouses at Minnesota for eleven years and have never been able to detect the slightest evidence of pathogenic change. Neither has there ever been any evidence of mutation in any of the other forms until recently, when some circumstantial evidence was obtained that one of the forms may be mutating. With such fungi as the rusts and the powdery mildews, however, it is difficult to demonstrate mutation, and to be certain that apparent mutations are not actually due to some other cause. Of course, physiologic forms of these fungi must have come into existence—because they now exist. There is no evidence that they were all specially created at one time and turned loose to plague unsuspecting and unprepared crop plants and crop pathologists.

Like varieties and forms of crop plants and crop pathologists, they probably descended in some way from preexisting forms: whether by slow evolution, sudden mutation, or by segregation from hybrids is a matter of speculation and not of precise knowledge. But it is likely that they came from some ancestral source, and probably still are coming, albeit they have thus far contrived to camouflage the road by which they came.

Another indication that physiologic forms of the rusts apparently are quite fixed is their geographical distribution. For instance, Levine and I have identified *P. graminis tritici* Form 27 from collections made in India, Hungary, France, the British Isles, and the United States. Form 21 has been obtained from Japan, France, Norway, England, the United States, and Canada. These forms probably have been in existence many years, because it scarcely seems likely that they could have been distributed so widely in a comparatively short time, especially since *P. graminis* apparently is not seed-borne. Many other physiologic forms of *P. graminis tritici* have been isolated from collections made in many different countries, and the parasitic behavior seems to be uniform and constant.

It is unsafe to generalize too much regarding mutation of parasitic fungi. Apparently it is extremely common in some species, but in others, such as the rusts and powdery mildews, it seems to occur more rarely or else it is difficult to detect it when it does occur.

The Relation of Physiologic Specialization to Epidemiology

A knowledge of physiologic specialization often is prerequisite to an understanding of the development of plant disease epidemics. For instance, the durum wheats have been introduced and grown rather extensively in the Dakotas, Montana, and northwestern Minnesota on account of their drought resistance and resistance to stem rust. For many years they escaped severe injury, even when bread wheats were heavily rusted. However, in some years they rust heavily. In 1923 there was a rust epidemic in the spring wheat region, and the durums in many localities were severely rusted. The explanation is simple. *P. graminis tritici* Form 11, which attacks the durums readily, was the predominant form that year. In 1925 there was again an epidemic, but there was very little rust on the durums, because Form 18 predominated and this form does not attack most durum varieties. Consequently, they were not appreciably injured by rust, while the bread wheats were injured severely.

It has been observed, also, that *Fusarium lini*, which, as Broadfoot and Stakman (16) have shown, consists of several distinct physiologic forms, is more destructive in some regions than in others. There is evidence that this may be due to the existence of different physiologic forms in those regions.

Physiologic Specialization and Quarantines

Physiologic specialization also should be taken into consideration in quarantine regulations. Certainly the physiologic specialization of fungi is not neces-

sarily the same in all countries. This has been strikingly shown by Reed (65) for smuts of oats. It also is true of some of the forms of *P. graminis*. Two outstanding examples may be given. For ten years Levine and I investigated the physiologic specialization of *P. graminis tritici*. During that time more than a thousand collections were made from many different countries. About 40 distinct physiologic forms could be recognized by their effects on 12 varieties of wheat, emmer, and einkorn. The only respect in which all of these forms acted uniformly was that all of them attacked Little Club wheat heavily and none of them could attack Khapli emmer normally. Then came a sudden and spectacular surprise. From a single collection of rust sent from Egypt, 8 distinct physiologic forms were isolated, and there seem to be prospects of still others. One of these forms attacks Khapli heavily and is scarcely able to attack Little Club at all, while another attacks both. Khapli has been used as a parent in a few crosses made in order to obtain rust-resistant wheats. They were not particularly important, it is true, but if the Egyptain form were introduced into the United States and became established here, Khapli might be just as susceptible as any other wheat or emmer. It also has been shown that there are physiologic forms of *Puccinia graminis avenae* (3). Three were found in the United States, but White Tartar oats was resistant to all of them. Many collections have been made but no form has yet been found on the North American continent which can infect White Tartar normally.[5] Therefore it has been used by plant breeders at Minnesota as a parent in producing rust-resistant, spreading panicle, early-maturing varieties of oats. These crosses have shown great promise. But forms of rust were obtained from South Africa and Sweden which are very virulent on White Tartar. Seed of White Tartar was sent to Doctor O. Arrhenius who grew this variety in the Experimental Fields near Stockholm, Sweden, and he reported that it was one of the most heavily rusted of all varieties. There is no particular reason why the Swedish or South African forms might not be brought into the United States on chaff and seed, on packing straw, or possibly on straw used for bedding animals. That is, there is no reason except quarantines. What is true of the smuts and rusts undoubtedly is true of many other pathogenic fungi.

The danger is particularly great in introducing seed-borne pathogenes. Foreign physiologic forms of *Fusarium lini* easily might be imported on seed flax, and they might be more virulent than any now here. The physiologic forms of this pathogene already in the United States cause us enough trouble without foreign reinforcements.

And then there are the smut fungi. There are physiologic forms of the smuts of oats, according to Reed (65), and of *Ustilago hordei* and possibly of *Tilletia tritici* and *T. levis* (33, 34), according to Faris. Rodenhiser and I have definitely demonstrated recently that there are forms of *Tilletia tritici* and *T. levis*, and there also are forms of *U. zeae* and probably of many other smut fungi. It would be the simplest thing in the world to bring these fungi into this country on seed.

[5] Recently evidence has been obtained that such a form may be present in Texas. (Unpublished results of cooperative investigations between the Minnesota Agricultural Experiment Station and the United States Department of Agriculture.)

The mere fact that we already have plenty of bunt on wheat in this country should not lull us into a false sense of security. *Tilletia tritici* is not merely *T. tritici*. It consists of several strains which differ from each other so greatly pathogenically that we might as well be dealing with different fungi.

Of course, the United States has no monopoly on harmless strains of pathogenic fungi, and, while we are taking precautions, it would be well for other countries to do so also. Surely we all have enough troubles now without permitting the promiscuous interchange of parasitic strains of plant pathogenes. We owe it to the agriculture of our respective countries to keep the population of plant pathogenes as homogeneous and harmless as possible.

Physiologic Forms as Biologic Reagents

Physiologic forms can render a service to agriculture to compensate for some of the damage and perplexity which they cause. They often have an uncanny ability to recognize varieties of crop plants. Therefore they may be useful. This is particularly true when the varieties of crop plants themselves differ mainly in physiological rather than morphological characters. Naturally, one of the simplest ways in which to detect varieties which differ from others in disease resistance is to inoculate them with the proper physiologic forms of the pathogene in question. For instance, it is easier to recognize Kanred, a rust-resistant variety of winter wheat, by its reaction to certain forms of *P. graminis tritici* than by the appearance of the plants in the field. Kanred often looks so much like certain strains of Turkey wheat that even an expert may fail to tell the difference. When seed lots are offered for sale, it often is quite impossible to recognize the variety. But it is relatively easy to recognize Kanred by its reaction to certain forms of *P. graminis tritici*. Vavilov (84, 85, 86), Dufrenoy (28), Aamodt and Levine (2), and others have called attention to the value of fungi as biologic reagents. But, as far as I am aware, the most important application in practical work was made by Johnston and Bower (46) in connection with the certification of Kanred seed.

Relation of Physiologic Specialization to Development of Disease Resistant Varieties

Physiologic specialization undoubtedly is most important in connection with the development of disease resistant varieties of crop plants. It has long been recognized that varieties may be resistant in one region and not in another. The phenomenon was often explained by assuming that soil and climatic conditions changed the resistance of the plants. While the effect of environment on the development of diseases cannot be overlooked and while its importance should not be minimized, much of the assumed variability in resistance of crop plants often is due to the occurrence of different physiologic forms of pathogenic fungi in different regions. This is perfectly clear with respect to the rusts and many other fungi. Marquis wheat, for instance, is very susceptible to black stem rust in the upper Mississippi Valley of the United States. In the Palouse district of the Pacific Northwest, however, and in some of the Southeastern States,

it is frequently extremely resistant, because there are few forms in those regions which can attack it normally. In 1926 there was a destructive epidemic of stem rust on wheat in certain regions of California, and Marquis was one of the most resistant varieties. There is circumstantial evidence also that flax varieties may react differently to wilt in different regions. There are physiologic forms of *Fusarium lini*, and the one at University Farm, St. Paul, was so virulent that in 1925 it injured even some supposedly resistant varieties, and in 1926 one of the few remaining resistant varieties is wilting badly at University Farm (15).

The first requisite in developing resistant varieties is to get intimately acquainted with the pathogene and its hosts. For instance, some investigators have stated that *Helminthosporium sativum* was virulent on wheat but not on barley; others that it was virulent on barley but not on wheat; still others that it was not particularly virulent on either. All of them were right. Dosdall (26) and Christensen found that certain forms attacked barley heavily but were relatively weak on wheat, while exactly the reverse was true of still others. Then, too, one can not draw final conclusions regarding the virulence of pathogenes without taking into consideration the particular variety of host plants inoculated. For instance, barley usually has been considered to be very resistant to, or immune from, *Puccinia triticina*. However, Schaal (70) at Minnesota found that some varieties of barley were moderately susceptible. Barley is not merely barley, any more than *P. triticina* is merely *P. triticina*. Recently, Cotter[6] has shown that *P. dispersa* also can attack some varieties of barley moderately. Others, however, are immune.

How can breeding work be successfully carried out when it is necessary to take into consideration so many physiologic forms? One of two things must be done, preferably both. Either it is necessary to study the number and distribution of physiologic forms of pathogenes against which resistant varieties are to be developed and then produce artificial epidemics with all the forms found in those regions for which the variety is intended, or the varieties or selections must be grown under conditions favorable for the development of the disease at many places in the region. In the one case one brings the forms of the pathogene to the plants; in the other, the plants are taken to the forms of the pathogene. A combination of the two methods is, of course, most desirable.

The difficulties of attempting to develop resistant varieties without taking into consideration physiologic specialization can be shown by some experiences in the attempts to develop varieties of wheat resistant to black stem rust. Mindum, a selection from Arnautka durum, was grown for several years at University Farm, St. Paul, Minnesota, and was practically immune from rust. However, when grown 150 miles from St. Paul, where there happened to be another rust form, it rusted fairly heavily. Kanred wheat is almost always immune in some localities, because the predominant physiologic forms do not infect it. However, in many regions Kanred is completely susceptible to black stem rust, which is not at all strange because there are more than 20 physiologic forms

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[6] Unpublished results of cooperative investigations between the United States Department of Agriculture and the Minnesota Agricultural Experiment Station.

which can attack it normally. Kota, a variety of hard red spring wheat, is very resistant to many physiologic forms of *P. graminis tritici* but is susceptible to others. And the expected happens. In some localities it remains almost free from rust, whereas in others it sometimes rusts quite heavily. Some Marquis-Kanred hybrids are sometimes very resistant under natural field conditions in certain localities; in others, however, they are entirely susceptible. Not only that, but they are susceptible in some years and resistant in others. It is necessary, therefore, to take into consideration the time factor as well as location.

Physiologic forms of the cereal rust fungi certainly are migratory, and epidemics are caused by certain physiologic forms in some years, whereas in other years they are caused by others. This means, therefore, that the surest progress in breeding rust-resistant cereals can be made by bringing all of the rust forms together and artificially inoculating the varieties with them. This is now being done in the breeding of rust resistant spring wheats.[7]

Furthermore, the varieties are being grown at various places in the Mississippi Valley in order to expose them to as many different forms as possible. The result has been much more rapid progress and a much clearer understanding of the problem than was possible a few years ago.

Many other examples might be cited to show the absolute necessity of knowing the number, pathogenic capabilities, and distribution of physiologic forms in order to make real progress in the production of resistant varieties. Attention already has been called to the fact that there are forms of *Fusarium lini* and that a variety which is resistant in North Dakota is not necessarily resistant in Minnesota. We have had similar experience with corn smut recently. The Sections of Plant Breeding and Plant Pathology of the University of Minnesota have been cooperating in the production of smut-resistant lines of corn. Some of the lines have been selfed for 7 or 8 years and fall into three classes: resistant, intermediate, and susceptible. When inoculated with the physiologic form from University Farm, St. Paul, they remain in their respective classes, but recently a form was obtained from Pennsylvania which caused heavy smut on some of the most resistant lines. And Nature, apparently in an ironical mood, decreed that some of the smut-resistant lines should be very susceptible to some physiologic forms of *Puccinia sorghi*, which in the past has appeared to be a rather well-behaved and non-aggressive pathogene. Surely the moral is clear. In developing varieties of crop plants resistant to certain pathogenes, we may be producing "physiologic forms" of host plants which are susceptible to other previously unimportant pathogenes.

Corn rust has not done much damage in the past. But some forms of this pathogene are decidedly destructive to some newly developed lines of corn. Supposing these lines were grown on account of their smut resistance. Rust might become as destructive as the smut was previously. There apparently is no correlation between smut resistance and rust resistance in corn; there are numerous lines of corn; and there are numerous physiologic forms of *Ustilago*

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[7] Cooperative project by the United States Department of Agriculture and the Sections of Plant Breeding and Plant Pathology, University of Minnesota.

zeae and *Puccinia sorghi*. Therefore, there are numerous problems in producing smut- and rust-resistant lines. Plant breeders and plant pathologists must know the forms of the host and of the pathogenes if permanent progress is to be made.

What is the hope of getting really resistant varieties of crop plants in the face of the obstacle offered by physiologic specialization? There are several facts which give us considerable hope that such varieties can be developed, provided all necessary factors concerning both the host and the pathogene are taken into consideration. In the first place, the same genetic factors may sometimes determine the resistance or immunity of a variety to several physiologic forms. Aamodt (1) has demonstrated this for the resistance of Kanred wheat to certain forms of *P. graminis tritici*. Kanred is immune from 12 of the forms described by Stakman and Levine. In crosses with susceptible varieties, immunity is dominant and the immunity from all 12 forms is governed by a single genetic factor. Consequently the problem is not always as formidable as it seems to be. However, Hayes, Stakman, and Aamodt (41) have shown that while immunity is dominant over resistance and susceptibility, susceptibility is sometimes dominant over resistance. In crosses between Khapli and Mindum resistance is dominant over susceptibility and the reaction to certain physiologic forms is governed by multiple factors, so that all types of reaction occur in the progeny. This again makes the problem appear complex, but there is the possibility of producing varieties synthetically which are resistant to most forms of a pathogene, or even to all of them. McRostie (57, 58) and Burkholder (21) used this method to some extent in breeding varieties of beans resistant to different physiologic forms of *Colletotrichum lindemuthianum*. The same method is being followed in the work at Minnesota in cooperation with the United States Department of Agriculture in the development of stem rust resistant varieties of wheat. For instance, Kanred, which is immune from 12 forms of *P. graminis tritici*, was crossed with Marquis. Immunity was dominant, and was governed by a single genetic factor. Consequently, some of the hybrid selections were immune from all the forms from which Kanred was immune. Selections from this cross were then crossed with Marquillo, a variety derived from a cross between Marquis and Iumillo. Iumillo, a durum wheat, is resistant to many forms and seems to be quite generally resistant in the field. Some of the selections from the cross look like Marquis but have some of the resistance of Iumillo. One of the best of these selections was named Marquillo and has been crossed with selections from Marquis × Kanred. Resistance to certain rust forms is governed by two factors, but the resistance of both parents has been combined in some selections from the cross. This is an illustration of the way in which it is hoped to build up resistance to many physiologic forms. It is true that a tremendous amount of work, both pathologic and genetic, is required in order to lay the foundation for work of this type. However, if it is not done in this way, it seems likely that the superstructure will be built on sands, and shifting sands at that.

The problem is simplified also by the fact that some varieties of wheat, notably Webster and Kota, often are resistant in the field to all physiologic forms of *P. graminis tritici*, apparently because there is so much sclerenchyma in the

stem, and the collenchyma bundles, in which the rust fungus grows, are so small that the rust pustules necessarily are small. This has been demonstrated by Hursh (44) and Hart.[8] Furthermore, Hart has shown that some varieties of wheat probably escape infection because the stomata remain closed so much of the time that the rust fungus, regardless of the physiologic forms with which the plants are inoculated, cannot enter readily. Thus, an apparently complex problem may be considerably simplified,—but how much is not yet known.

Will disease resistant varieties retain their resistance permanently? There seems to have been a general impression that they would not, but the explanation usually has been that they lost their resistance on account of a change in physiology caused by altered environment. It is, of course, true that resistance, or apparent resistance, of some varieties of crop plants may be affected profoundly by environment. The investigation of Jones (47) and others on yellows–resistant cabbage, of Tisdale (82) and of Barker (4) on wilt-resistant flax prove this definitely. And the extensive investigations on the effect of environment, particularly soil temperature, made at Wisconsin and elsewhere show how variable disease resistance sometimes may be. But there is a wide difference between phenotypic fluctuations in resistance and a permanent or genotypic change (Tisdale, 82). However, it has been shown conclusively that resistant varieties often apparently lose their resistance because of exposure to different physiologic forms from those with which they were inoculated when it was concluded they were resistant. As it has been shown that physiologic forms of some fungi mutate, that new ones may be introduced into new regions, and that they may possibly originate by hybridization, what steadfastness can we expect from resistant varieties in the face of the insidious attack of many and changing physiologic forms? This question must be investigated and answered by the historical method. We know that varieties sometimes appear to be resistant for a long time and then, either suddenly or gradually, appear to lose that resistance. Whether they become more subject to disease on account of the introduction of new physiologic forms of the pathogene, or because of the appearance of unusually virulent mutants, cannot be answered at present. It is known, however, that such apparent changes in varietal resistance do occur. One of the most important recent contributions is that of Tisdale, Melchers, and Clemmer (83) with respect to *Sphacelotheca sorghi*, the kernel smut of sorghum. For many years, milo, hegari, and feterita were almost immune from kernel smut, both when inoculated artificially and when grown under natural conditions. But in 1923 kernel smut was found on milo in some localities in Kansas, New Mexico, and Texas; and in 1924 it was found both on milo and hegari. It was shown that the form of smut on these two varieties was different from that which occurred in the regions in which the varieties did not become smutted. The newly discovered form infects milo and hegari but not feterita. These varieties apparently lost their resistance. But they actually did nothing of the sort. They are just as resistant

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[8] Unpublished results of an investigation by Helen Hart at the Minnesota Agricultural Experiment Station, in cooperation with the Office of Cereal Crops and Diseases, United States Department of Agriculture.

to the original form of the smut as they ever were. The fact simply is that another form of smut appeared; and this form can infect them. Whether this new and virulent form arose from a form already in this country, or whether it was introduced, cannot, of course, be answered; but the experience is a real contribution to the historical method of studying the so-called permanence of resistance in varieties. There have been other similar experiences in the past; and there probably will be many others in the future.

Physiologic specialization, then, is extremely important in several ways: It must be taken into consideration in systematic work with fungi; it explains many apparently contradictory events in plant disease epidemics; physiologic forms often can be used as valuable and precise biologic reagents; and a knowledge of physiologic specialization is highly important in the control of plant diseases, particularly in relation to quarantines, and in the breeding of disease-resistant varieties. The elucidation of the problem of physiologic specialization furnishes at the same time discouragement and hope to those who would breed disease-resistant varieties of plants. Just how great an obstacle the phenomenon will be cannot be stated. This much, however, is certain: a thorough knowledge and use of physiologic forms is basic to sound work in the development of disease-resistant varieties.

It may possibly seem to some that the complexities and difficulties caused by physiologic specialization of pathogenes have been overemphasized in this paper. I do not think they have. The problem is puzzling and complex: how puzzling and complex can be appreciated adequately only by those who have puzzled long and risked developing complexes of their own in this field of research. It is to be hoped that none will infer that a hypothetical mental complex has caused a distorted view of the whole problem of disease resistance and epidemiology, which has many phases. I have tried merely to call attention as sharply as possible to one phase: the absolute necessity of knowing the physiologic specialization of pathogenes in order that our work may have greater definiteness and precision. Physiologic specialization is one of the extremely important phases of plant pathology and, as such, must be taken into consideration in present and future work.

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THE INFLUENCE OF SODIUM ARSENITE, SODIUM CARBONATE, AND FORMALDEHYDE ON THE CONIDIA OF ERYSIPHACEAE[1]

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In America and in France compounds of arsenic have long been used in fighting insects destructive to plants. Attempts to use them against parasitic fungi have been made—up to the present—only in Poland and in Russia.

The purpose of this study was to show the influence of sodium arsenite, sodium carbonate, and formaldehyde on the germination of the conidia of Erysiphaceae.

To this end a series of laboratory experiments was made with conidial spores of *Erysiphe Polygoni*, *Sphaerotheca pannosa*, *S. Humuli*, *Oidium quercinum*, and *O. Evonymi japonicae* with the following result: The germinative power of the conidia is highly variable and dependent upon the degree of maturity of the conidia, the period of their germination, and upon atmospheric conditions. More than once, the percentage of conidia which germinated even in water was small, while solutions of arsenical compounds had an inciting effect. The approach of the period during which the perithecium is being formed lessens the germinative power, as their vegetation ends then. Tests with conidia of *Oidium quercinum* which, in Poland, do not reach the stage of forming ascus strains have confirmed this, as these germinate even at an advanced moment of their vegetation period. The number of germinating conidia in a drop of liquid depends also on their distribution within the drop; for instance, conidia gathered in groups show a better germination power than single specimens.

In the first stage of the experiments, solutions employed by Dr. J. Trzebiński[2] and others were used, namely, 0.008, 0.01, 0.02, 0.03 per cent sodium arsenite, but in all of these solutions the conidia germinated and after 24 hours the germ-tubes had reached a length of about 160μ. Experiments made in 1922 had shown that 25 to 27 per cent of the conidia germinated in a solution containing 0.05 and 0.01 per cent of sodium arsenite. For the experiments conducted in 1923 the solutions used are shown in Table 1. The conidia germinated in all these solutions, and the following results (Table 1) were obtained:

[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 19, 1926.

[2] Trzebiński, J. Influence de l'arrosage des groseillers verts (Ribes Grossularia) avec diverses solutions d'eau des préparatifs chimiques dans la lutte contre le champignon Sphaerotheca Mors-Uvae Berk. et Curt. Mém. de l'Institut National Polonais d'Econ. Rurale à Putawy. Krakow, 1921.

TABLE 1. GERMINATION OF CONIDIA IN SODIUM ARSENITE AND SODA

In 0.5% sodium arsenite	13% germinated
" 1% " "	6.5% "
" 2% " . "	3% "
" 0.5% and 1% soda	6% "
" 0.01% sodium arsenite 0.5% soda	15% "
" 0.025% . . 0.075%	16% "
" 1.3% formaldehyde	12% "

At the same time the percentage of conidia germinating in water reached 21 per cent. From the above it may be deduced that the higher the concentration the lower the number of germinating conidia. These solutions, however, are too strong for practical purposes, as 0.05 and 1 per cent sodium arsenite burn the leaves, and formaldehyde has no influence on the disease. Only soda, even if applied in solutions of 1 per cent, did not damage the leaves.

Together with the calculations of the number of the germinating conidia, the length of the germ tubes was measured. It varied in accordance with the solution in which they germinated (Table 2).

TABLE 2. LENGTH OF GERM TUBES IN THE SOLUTIONS TESTED

Solution, per cent	Length of the germ tube, in μ
0.3 sodium arsenite	64, 122, 160
1.0 " "	33
2.0 " "	15, 18, 25
0.5 soda	70, 90
0.01 sodium arsenite 0.5 soda	90
0.025 sodium arsenite 0.075 soda	75
1.3 formalin	63
H_2O	100, 150

From this table may be seen that weak solutions exert a small influence on the germinative power of the conidia.

Further tests are shown in Table 3.

TABLE 3. GERMINATION OF CONIDIA

Solution, per cent	Percentage of germinating conidia
0.5 sodium arsenite	18
1.0 " "	13
2.0 " "	8
0.5 soda	23
1.0 "	13
2.0 "	10
H_2O	30

As the conidia germinated even in these solutions it was decided to use stronger concentrations until the desired effect was obtained, that is, until the conidia would cease germinating. As a result the observation was made that the per-

centage of germinating conidia varied proportionally to the number of conidia germinating in water. The higher the germinative power of the fungi the smaller was the effect of the various solutions on them. The power of germinating, however, is highly dependent upon atmospheric conditions, as illustrated in Table 4.

TABLE 4. GERMINATION OF CONIDIA UNDER DIFFERENT CONDITIONS

Solution	Percentage of germination	
	July 4, 1925	July 25, 1925
3 sodium arsenite	2.4	9.6
5 " "	0.8	7.0
8 " "	0.4	2.3
10 " "	0.2	2.9
H^9O	18.2	37.0
3 sodium carbonate	5.0	8.0
5 " "	2.5	2.2
8 " "	1.1	1.2
10 " "	0.3	0.4
H^9O	13.7	25.0

In a solution of 15 per cent sodium arsenite and in a solution of 15 per cent sodium carbonate the conidia do not germinate.

INTERNATIONAL PLANT DISEASE LEGISLATION— IS IT PRACTICAL?[1]

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Plant pathologists, entomologists, and biologists generally, interested in the problems of plant disease legislation and quarantines, would be well advised, if they wish to satisfy intending importers of plants or plant products, to study, carefully analyze, and demonstrate, if possible, the advantages to any country's resources that have been the result of the enforcement of plant disease legislation, both in relation to domestic and international traffic and trade.

I take it for granted that few or none will dispute that most of our plant protection methods in this direction have come many years too late. Diseases and insect pests have traveled far before the days of embargoes and restrictions, and many have become cosmopolitan, however undesirable they may be. We have, in each country, a goodly number of pests and diseases that require all the attention pathologists and entomologists are able to give them, nor can there be much doubt that had it not been for the presence of seriously destructive insects and pests, very scant progress would have been made in sanitation generally in the production of agricultural and horticultural crops, in control methods, in the study of disease resistance, or in general applied related researches.

This being so, it must be admitted that diseases as well as insect pests have proved a blessing in disguise. For instance, the discovery of powdery scab some fourteen years ago on the continent of America gave the impetus to a system of certification and inspection of seed potatoes now widely established, the practical value of which to the farmers can scarcely be overrated. Incidentally, and apart from the production of disease-free seed potatoes, there has been marked progress in our knowledge of potato diseases and of their control, and consequential appreciable reduction of losses caused by the same. Would such have been the case, or would the progress made have been equally steady, had we not had powdery scab to contend with? In Europe powdery scab has been known for years; it is regarded with comparatively little concern, and practical measures for its control have scarcely been worked out, with few exceptions. On the continent of America I believe that we may say that powdery scab today is a disease of minor importance, simply because of the thorough knowledge we have of all aspects of the disease. Our researches have practically conquered this foe.

A good many countries are prominent in the scientific study of the causes of disease, but sadly backward in the adoption of proper control measures,—in which direction, principally, other countries lead. Without wishing to underrate

the services of the plant pathological or entomological student, the first duty to be rendered to the agricultural industries is in placing at the disposal of the general public advice on the control of diseases and pests by the most up-to-date and economical measures; for, the lower the cost of crop production, the higher the net returns.

In addressing myself to plant pathologists it seems hardly necessary to quote more of the many claims that could be advanced in support of the statement that the presence of plant diseases often proves a blessing in disguise. Wherever we look we can find such instances.

The above considerations raise this question: Would agriculture, horticulture, forestry, and related industries have the same advances to record, had there been no insect pests or plant diseases, that required or rather compelled intensive study, and had not such studies led to the establishment on a much sounder and more sanitary basis of our basic industries like agriculture? The determining of the value of a well organized plant pathological or plant protection service must essentially take such factors into consideration. I may say that the compulsory study for the reason of national welfare of one destructive disease or pest, and even more the ultimate success in controlling such situations, have led on to the study of others, until, gradually, both plant pathology and entomology have become recognized as the invaluable aids they really are today in world agriculture.

Furthermore, the free and unrestricted importation of plants and plant products enjoyed—if I may use such a term—for many years, not so long past, has given to this continent its fundamental start, at any rate, on the road to success in agriculture and horticulture which we now enjoy, and, doubtless, the same may be said also of other comparatively new countries. Emigration to and settlement in the world's remotest corners have undoubtedly been followed by old world practices accompanied by old world stock. Partly rivalry, partly acquired knowledge of superior varieties, or even mere sentiment, have led and are today leading to progress in these basic industries with all, or most nations.

Grape vines would not, probably, be grown today in the Niagara peninsula had it not been for the pioneer efforts of a German emigrant, who practically established this now vastly important industry by bringing along with him some stock from the Rhineland of Germany. Plant inspectors are aware that such practices, that is, importations by immigrants in their effects, still prevail, and will prevail as long as there is sentiment and love of the motherland in the human heart. So all nations, but more especially the newer nations, have to acknowledge their indebtedness for their progress along agricultural lines to the original importations of plants or plant products, seeds or nursery stock, brought in by their ancestors. It is, therefore, most emphatically to be condemned when any protective service exceeds its legal and moral rights to the extent of prohibiting such importations within reason by private effort. Every human being is more or less of an experimentalist, and thousands of our most valuable varieties of grains and fruits, agricultural products, plants, animals, machinery, etc., owe their origin to other countries. Marquis wheat—the most important wheat today

in America, and, indeed, in world agriculture—where would it have come from but for the wise foresight of the late William Saunders, the founder and first Director of the Experimental Farms of Canada, who brought varieties of wheat into Canada from all over the world?

Something may very emphatically be said in support of permitting wise and safe importations by all who have the progress and development of their own interests at heart, for, all said and done, no one can for long withhold from a nation the benefits personally derived from such individual efforts. The plant quarantine bodies of many countries may be well advised to ponder whether too stringent rules may not prove a great and serious hindrance to progress in the long run.

True, nowadays, scientific men or *bona fide* experimentalists, are permitted—at any rate in Canada—to bring in any plant or plant product under general quarantine for scientific purposes. I understand, however, that in some countries, like privileges are not so freely granted, and, where such is the case, it might be well to modify the rules and regulations as soon as possible. For no committee or board can morally have the right, far less the fore-knowledge, to state that a new introduction will, or may, not benefit a nation far more, directly or indirectly, than the possible or problematical introduction of a new disease may work its injury.

I regard such a decision as a grave responsibility upon the shoulders of any quarantine official, for there is just the same chance for either of the two events occurring, that is, that any given new importation may turn out a blessing or a curse to a country. Besides, in the event of such an importation introducing a new disease or pest, where is the efficient plant protection service that should protect all crops and resources from being destroyed by such agencies?

The dilemma posed above gives pertinence to my next consideration: Can plant diseases and insect pests be effectively kept out of a country? My own experience would lead me to answer this query in the negative, but with some slight reservations. We all know that plant inspection at the ports of entry affords but a poor guarantee. For one thing the cost for maintenance will not stand comparison against the doubtful benefits derived therefrom. Doubtful benefits—and, to speak truthfully, comparatively few are the interceptions that are achieved during the all too short and busy season during which importations are possible—do not adequately repay the requirements of the case, unless the inspection service be so far enlarged as to become unwieldy to handle. Every conscientious inspector of plants or plant products, I am sure, has similar doubts in his mind. Here may I observe, lest the above remark be construed as a reflection on the inspection service in Canada, that I believe Canada has an up-to-date inspection service, such as few can equal.

May I now ask your consideration of the following question: Have plant disease legislations and port-of-entry inspection services been able to justify their existence; have they materially contributed to the national wealth of any country, or materially assisted in protecting the resources they sought to protect? In other words, is the cost of maintaining these services, as at present constituted,

warranted, and what claims can be advanced that, without them, things would be far worse than with them?

Remember that, opposed to the questionable benefits to be derived from the miantenance of such services, with their essential tendency towards keeping plants out of a country owing to the possibility of introducing costly pests and diseases, which have already been introduced by the hundred, if not thousand, and that, too, despite quarantine measures, there is the benefit, which it is equally reasonable to expect from the success of a new introduction in advancing the progress of agriculture and related industries. The more workers we can induce to interest themselves in such aims, the more immediate are the results likely to be.

Perhaps the most conspicuous and best known Board, charged with the duties under discussion, is the Federal Horticultural Board of the United States. The tendency of the day is towards international plant disease protection, and my present purport is to analyze the value of this work we are all engaged in, hence nothing is farther from my mind than to reflect on an institution of this great and noble nation, our host, yet the records of this organization, whose functions are almost unique in the world, should enable an answer to be made to this delicate question fully and convincingly. Have the United States—the public in whose interest the Board functions—derived economic benefits on a strictly biological basis commensurate with the expenditure incurred to attain those biological aims?

I know that the point I am now trying to make is a delicate one,—possibly none of us could off-hand state that any nation we here represent is entirely guilt-less in the matter. But, since the decision of this point vitally affects the future of international plant disease regulations, will you pardon me if I speak quite plainly, and believe me that my object is to raise no tariff storm, but merely to disentangle the biological objects of plant disease legislation from the tariff objectives too often cloaked under biological disguises.

One important result of such a disentanglement of biological motives from all biologically irrelevant matters I will just briefly outline here. We all know to our cost that our decisions, however impartial and strictly biologically founded we endeavor to make them, are subject to challenge or expostulation, shall I say, by dissatisfied importers, who turn away convinced—rightly or wrongly—that they are the victims of autocratic ruling on the part of the authorities. Were the decision capable of being clearly shown to be given solely on biological grounds, that importer might, nay very probably still would, be dissatisfied, as it is only human to revolt against any kind of law,—but he would have no grounds for assigning any ulterior motives to a ruling given against him. We should thus establish confidence on the part of the general public in the imparti-ality of inspection services—a most important factor in governmental dealings,—instead of the present often veiled hostility. Gentlemen, we are like the mice of the old fable, who will bell the cat?

The question is essentially one for a learned economist to study and answer, and in these days of efficiency of service, it should be possible to determine this

point. And if inspection services be weighed and found too light, or rather too top-heavy, from the viewpoint of economy, how could such, or similar services be reorganized in order to conform to the precepts of "lowest production costs." This would indeed be a worthwhile investigation, a sort of stock-taking of our own importance, upon the result of which will depend the future attitude alike of inspection services towards the public, and of the public towards the services, whether in the domestic or the international fields. Is domestic plant inspection service practicable or not, and for the same reasons, or under what conditions, are international plant disease regulations practicable or the reverse? If it costs more to fight a disease of a certain crop than the crop itself is worth, is that a sound undertaking? What should be the aims of services that would protect a country's resources, natural or developed?

The question of domestic quarantines may here be briefly mentioned. They consist mainly of measures designed to confine *pro tempore* and within a defined area the progress of any disease or insect pest, or to afford time for investigation and control. In this respect they are often of immeasurable value; they subserve the aims of the investigator by affording him time to work out his control measures, whether such be preventive, curative, or dependent on the development of resistant varieties. Under certain circumstances research work may keep pace with the spread of disease confined within such quarantined areas, though generally the areas require to be enlarged from time to time, depending largely upon the nature of the trouble. Above all, time is afforded for the settlement of the most important matter of all, namely, investigations relative to control of the pest or disease in question. In this way domestic quarantines are normal aids to the investigator.

Usually they are difficult to enforce, even in countries of immense areas, such as the United States and Canada, between which countries happily cooperation is most intimate, but even here the economic question is the decisive factor. Thus, in the matter of control of white pine blister rust, in British Columbia we have no similar interests, nor anything like the interests to protect that the United States have south of our border there. Consequently, by us it is considered sounder economy to devote to other phases of work monies which might be expended in fighting this disease for the benefit of our good neighbors. Could any Government be expected to be so unselfish and generous as to devote vast sums of money to work largely for the benefit of the government of another country, unless it is a matter of trade relations pure and simple? That time has not yet come—nor is it likely to come for a year or two, more or less.

The domestic quarantine thus is a complement to research and active plant disease control, and so serves its purpose within reason.

Now as regards the aims or nature of foreign quarantines. Invariably such a quarantine is set up when a disease of foreign origin, or suspected foreign origin, is discovered. The simplest step is to prohibit the importation of all materials likely to further introduce the trouble in question, a tendency inclined to the course of least resistance, but biologically of questionable soundness. This often gives rise to serious disturbance of trade with the countries affected

by such a quarantine, and is frequently resented not only by those countries, but also by one's own nationals, who find their individual interests vitally affected as a consequence of a quarantine imposed.

On the other hand, it cannot be denied that, in some cases, such quarantines or embargoes have a similar effect to that of a protective tariff, and are welcomed by interests consequentially benefited by an otherwise ill-wind, that blows nobody any good. It is also true that there are interests which will exaggerate the importance of a disease or pest, and thus arouse and secure the support of the mainly indifferent and unsuspecting public—in all countries alike, the ultimate consumer. The latter knows little about such measures, but pays dearly for that lack of knowledge.

It might be argued that the presence of a yield-reducing or otherwise destructive pest will equally affect the consumer's pocket by a rise in price of the product concerned. True! But that is where the plant pathological services step in to restore the normal equilibrium by devising means for fighting the pest, and after more or less of an interval they are generally successful. Thus, the devastation wrought by the chestnut tree blight undoubtedly gave rise to the utilization of other woods nobody would have thought of otherwise, and incidentally it made well worth while a general active campaign which resulted in widespread efforts to protect and conserve other natural resources. This is a problem for the political economist—an indirect benefit resulting from an undoubted pest. Where lies the balance of loss or gain?

Incidentally, every country suffers damage from the diseases of other countries. Before this truth became evident, plant pathology and entomology as applied sciences were largely more systematic than economic. The danger with foreign quarantines is that they usually go too far—it is a human tendency to be too drastic when in power. There can be but little doubt that a vigorously fighting service will achieve more results than a doubtfully preventive service. It is natural to become alarmed at many things, but frequently regulations are promulgated which are unnecessarily unreasonable.

For example, let us take the question of potato importations into and from Europe. Europe excludes potatoes coming from the continent of America because of the dread of the Colorado beetle. Yet it is extremely questionable whether this pest is at all likely to be introduced with potatoes. Many are the thousands of bushels examined during our Dominion-wide inspection service, and it has yet to be proven that the beetle is ever present, or likely to be so, in or amongst potatoes. The fact that the beetle was found during the Great War in European countries is no proof that it came over with potatoes. Indeed it may have come over in the most unlikely material: Where should one draw the line? That is really a most important question. Accidental importations are likely to take place, nay, have taken place, of all sorts of pests and diseases. I myself, some years ago, found viable spores of a smut in Japanese toys made of bamboo. Would it not be biologically sound to admit potatoes originating in America into Europe, since it is biologically as well as practically sound that

potatoes, at any rate for the table, do not constitute any menace because of the Colorado beetle.

Equally I am of the opinion that the authorities of the continent of America might well reconsider their embargo against European potatoes on account of the wart disease. On a biological basis, in view of the many varieties of potato absolutely resistant to wart disease, the reason for the exclusion is no longer quite so sound as it was when the embargo was instituted. It is a disease of exceedingly slow progress, and may be kept uner control by the use of resistant varieties. Such varieties might quite reasonably be admitted both into the United States and into Canada, providing there is a market for them. But the doors should no longer remain closed; that is neither reasonable nor biologically sound. Open the doors for importation, subject to certification by responsible officials that the variety is truly immune, and that the disease is not known within a radius (to be definitely determined) round the spot where the crop was grown. Matters of trade expediencies are not the concern of biological services; they can very well be left to establish their own equilibrium, which they will very quickly do.   —

As exemplified in the above-cited case of potatoes, every country might well go over its regulations and, on a truly biological basis, decide the respective merits of its many regulations in force at present. Such a revision is most desirable from many points of view, and should, if possible, be the foremost duty to be performed by any International Advisory Committee set up. In this matter I see much to be gained from international concerted and cooperative action. The Phytopathological Section of the International Institute of Agriculture would indeed render a valuable service, if it would take under review the present rules and regulations in force in all adhering countries. I must confess that personally I am in favor of the biologically open door. I do not know who uttered it, but this saying appeals to me: "Many people can do things if kindly encouraged, but give me the man who does things in spite of hell."

I submit that the first step that should be taken is to have an International Committee appointed to discuss the merits of the present regulations in force with a view to modifying those too severe and discontinuing those that no longer have behind them biological reasons, as formerly when they were conceived. Naturally such a committee should only be concerned with biological considerations and, therefore, be composed of technical experts of experience.

We cannot deny that gradually inspection services at the port of landing will come to an impasse; they have nearly reached such intolerable conditions nowadays. There are reasonable men outside of inspection services, whose opinions are as valuable as those of men within the services. At present the tendencies are to be autocratic beyond the avowed biological principles involved.

It should be easy to agree on the principles which should underlie international cooperation. Anything that is affected by disease or insect pests has no business to be offered for export. Surely, if we are all honest in our efforts towards improving present practices, we could at least agree on that reasonable primary important condition.

It is of interest, in this connection, to review the laws of various countries regulating domestic exchange, or sale of plants or plant products. Most countries have enacted laws standardizing their fruit, grain, potatoes, roots, etc., and anyone contravening such Acts is fined; but no country includes or applies the regulations to the same commodities when intended for export, and few of them demand that all importations should at least conform to the standards by which domestic supplies are regulated. Inferentially, this indicates that things not up to the standards for domestic use are good enough for export to countries willing to take them.

The next point for international consideration then should be to make commodities offered for export conform to the domestic requirements, at least. With this object in view consideration should be given to the question of standardizing all commodities readily standardizable. May I here refer to an example that may serve to illustrate the point? In Canada we have, possibly, seed potato certification standards that are the most severe of any in force throughout the entire world, and these are as follows:

INSPECTION STANDARDS FOR CERTIFIED SEED 1926

FIELD

1926 Standards

Blackleg.. 1st insp.	4%	2nd insp	2%
(Leaf roll (curly dwarf, etc.))................................. " "	2 "	" "	1 "
Mosaic.. " "	2 "	" "	1 "
Wilts... " "	4 "	" "	2 "
Foreign... " "	1 "	" "	½ "
Misses (unless due to blackleg or mechanical causes)............... " "	2 "	" "	2 "

Providing that in no case shall a total of more than 8 per cent be allowed on first inspection and more than 4 per cent on second inspection.

TUBER

1926 Standards

Wet rot (bacterial)...	1%
Late blight and dry rot...	1 "
Common scab and Rhizoctonia—severe...........................	5 "
Powdery scab.	1 "
Necrosis, wilts, and internal discoloration, other than due to variety..............	5 "

Providing that in no case shall a total of more than 8 per cent be allowed.
Not more than 2 per cent of the tubers shall be badly off type or damaged by sunburn, cuts, cracks, bruises, insects, etc.
No frost injury or foreign tubers shall be allowed.
Not more than 5 per cent by weight of the tubers shall be below three ounces or above twelve ounces.

We find it to our interest to offer potatoes of exactly the same standards to any country wishing to have and pay for them, with most excellent results, as may be known to our very good friends and hosts of the United States. You will, I think, agree that hardly anything better, in carload lots, can be produced.

Equally, our domestic standards for table potatoes are of a high order, and I am positive that no objection could be raised to the grades therein defined by any service, be it ever so exclusive. Our organization enables us to maintain these standards; and I contend that these regulations prove by their practical results to be worthy of a wider application, since they lead eventually to the desirable condition that the domestic regulation of the export of anything affected

by disease should be the foremost principle of international trading in plants or plant products.

We are now, also, practising a fairly extensive certification of raspberry nursery stock, yielding stock practically free from destructive diseases. The question of certification of seed and elite stock has been developed to such an extent in some countries that it is now but one step more to reach the realization of the basic principle outlined above, which benefits not only the country itself, but also the countries with which it trades in such commodities.

Naturally there are still countries where efficient inspection services have not yet been established, and these countries will either have to provide such services, or forego the benefit of trading with other countries that insist upon disease-free importations according to standards internationally accepted in principle. Be it noted, too, that then the refusal of any country, implicitly or explicitly, to accept imports conforming in all respects to its own domestic standards on the same terms as for similar products of its own nationals, can be ascribed to but two reasons. The one is a strictly biological reason, a distrust of the capacity of the inspection service of the exporting country—for, obviously we cannot credit a country with distrust of its own institutions—the other, a purely fiscal reason, a desire at all costs to exclude competition with its own products. I here offer one suggestion towards belling the fiscal cat, as referred to above.

Can anyone here doubt but that potatoes of the type produced under our certification would be acceptable to any country truly desirous of opening its doors wide to any plant or plant product of a similar degree of freedom from disease?

I can see that, gradually, we may have to agree on these points. No nation can afford to become exclusive, and it seems to me that the suggestion offered should be given full consideration as an alternative to the present system of closing one door after another, a system which leads to antagonisms and resentments, besides affording no solution that has the least claim to being biologically sound, of the underlying problem.

In concluding may I say that I have striven to avoid the criticism of offering purely destructive suggestions, and may I once more emphasize my point that at least *a* solution of the perplexing problem of international plant disease legislation may be found along the lines I have constructively endeavored to indicate. I can see no reason why we should not all give this suggestion careful consideration, and so be in a position, when next we meet, to formulate regulations that will afford safe and liberal interchange of products among nations, instead of arousing antagonisms, as at present, and leading nowhere in particular.

THE BIOLOGICAL BASIS FOR THE INTERNATIONAL MOVEMENT OF PLANTS AND PLANT PRODUCTS[1]

INTERNATIONAL COOPERATION IN SCIENTIFIC RESEARCH AND THE INTERNATIONAL EXCHANGE OF PLANTS AND PLANT PRODUCTS

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I have been invited to speak here on the biological basis of the international exchange of plants and plant-products.

I dared to accept this invitation, not because I hoped to be able to give here a satisfying solution of this very important but no less difficult problem, but because I was asked to speak on the *biological basis* of the problem.

For it seems to me that the basis on which the problem ought to be founded is sometimes lost sight of owing to the difficulties attending an attempt to solve the problem.

Only when the value of the basis of the problem has been kept in mind will there be any possible chance that in the future a solution of the problem will be found by a close international cooperation, based on mutual appreciation and confidence.

Biology is the doctrine of life on earth and includes all living creatures, men as well as animals and plants, and it especially regards all parts of the globe.

When the Creator made the earth, He made the whole of it, He correlated the different parts of it and the products of one part of the earth are necessary to the inhabitants of another portion. And this does not only concern the products of agriculture and horticulture.

Life has become so complicated that no country in the world is still to any extent self-supporting. A country that has an abundance of coal, oil, minerals, and has big industries generally does not produce large quantities of agricultural products. On the other hand, it is necessary for a country producing agricultural products to exchange these for coal, oil, minerals, and the products of industry.

The prohibition of the exchange of the products of agriculture and horticulture will automatically also put an end to the exchange of the products of the industries or the raw materials.

The exchange of those different kinds of products is inseparably connected, and life on earth is only possible by an international exchange of commodities of all kinds.

This is a natural truth and a natural law and the violation of this law must disturb the economic balance of the world. Every transgression will have its reciprocity till there will be a hopeless chaos.

At some time this will become also fatal to him who in the beginning seemed to take advantage of the disturbance of the balance.

If I have been sufficiently clear in the foregoing, it will be understood that the international exchange of agricultural and horticultural products is inseparably connected with and only forms a link in the chain of the international exchange of commodities that is the foundation of life on earth.

We have to keep this in mind and we have to consider this truth as the principal biological basis of the problem of the international exchange of plants and plant products.

The fact that the program committee of the International Congress of Plant Sciences has put this problem on the list shows that those men consider this problem as a very important one, with an international scope.

I think this problem is so important for the international relation of scientific investigators that its significance is only matched by the difficulties that are connected with the solution of the problem.

Only if the difficulties are analysed in a purely scientific way and the synthesis built up on purely scientific arguments can there by any hope of a satisfying result.

And as it is a problem of great *international importance*, it can only be solved by international scientific cooperation.

Secretary Hughes in his address at the opening of the annual convocation under the auspices of the American Association for the Advancement of Science in Washington in Dec. 1924, dealt mainly with the advantages of cooperation, pointing out that scientific achievement is not individualistic, but is the work of groups, either consciously formed, or produced by the essential correlation of effort. Such cooperation, he maintained, is of necessity international in its scope. "We should think in terms of the cooperation of peoples and not simply of governments. Science knows no political boundaries; she recruits her conquering chieftains from all climes and races. It may be an Austrian monk, revealing the secrets of plant inheritance; or a New-Hampshire farmer's boy, who learns to fashion instruments of the utmost delicacy and precision; or a Serbian herdsman taking youthful lessons in communication by listening through the ground; or a Japanese devotee of medical research isolating and cultivating microorganisms. In this field all are co-workers, and pride is not of race or of tradition, but of achievement in the interest of humanity."

I think we must take the foregoing wise words as a guide, if we try to find a way for the solution of the difficult problem which occupies us here by international cooperation.

What difficulties can arise by an entirely free exchange of plants and plant-products? There is the danger of the transportation of plant pests and parasites.

We phytopathologists have the task to protect agriculture and horticulture in the whole world. As a matter of fact, in the first place we have to protect our own crops against foreign as well as against domestic parasites.

If there is any danger connected with the international exchange of plants and plant-products, we have to make this danger as light as possible. We have not only the right, but we are even obliged to ask from importers of foreign

plant-products a reasonable freedom from diseases of the products they want to import. However, we must keep in mind that the exchange of plant parasites has always occurred in the past and will always take place in the future.

The evolution of human intercourse has continually increased the chance of this exchange of parasites, and international relations are entirely impossible unless reasonable chances be taken. Even an entire closing down of all human intercourse would not prevent this interchange of plant parasites. Moreover, the closing down of this intercourse as well as the prohibition of all plant importations, would be entirely inadmissible on biological grounds, even if it should prevent the exchange of parasites.

When I use the word inadmissible I must be clearly understood. No international agreement can be founded on a sound basis when one party forces his opinion upon the other. Either retains his independence in his own domain.

However, if we consider the matter from a fundamentally scientific standpoint, only an argument founded on scientific grounds can be accepted. For this reason, in point of principle we must immediately exclude all motives which might be due to the wish to protect domestic cultures by excluding foreign competition. Economically these are admissible tactics, but they belong to the domains of social economics just as the protection of any product of industry. They have nothing whatever to do with scientific arguments for the exclusion of plant parasites. We can not discuss here the pros and cons of free trade and protection.

Likewise, we have to exclude all measures which aim at using phytopathological arguments reflecting on the quality of the products. This too belongs to the domain of trade and the supply of inferior quality will never pay, owing to competition. We have only to consider the purely phytopathological side of the problem inasmuch as this is founded on entirely scientific grounds. Many famous Phytopathologists have already discussed the economic as well as the technical side of the problem in various important publications. For example—Jones, Orton, Shear, Reh, Ritzema Bos, and others.

One of the best and most lucid expositions of the difficulties of the problem is undoubtedly the address of Güssow at the International Phtopathological Congress at Wageningen in 1923. Rightly he points to the necessity of trying to understand each other's difficulties before an attempt to come to a satisfying solution can be thought of. My feeling is that this will be possible if all adhere to the biological basis of the problem, if the restrictions of the free exchange do not go farther than is absolutely necessary for the protection of the home crops against plant parasites, and the arguments for exclusion are based on purely scientific phytopathological grounds.

Science is international and knows no borders. What is true for the scientist of any nationality will be true for every scientist in the world. As long as this is kept in mind, there cannot be any possibility of bad feelings between the scientists of different nations, even if for a short time their interests seem to clash, and we need not be afraid of searching for arguments for the exclusion of each other's products in retaliation.

The interest of the exporting as well as of the importing country entails that a well founded objection against a product which is to be exported should be removed as soon as possible. As both must be interested in a free exchange of the product without unreasonable risks for one of them, there will be a sound basis for international cooperation, if this aims at canceling the restrictive measures as soon as the objections have been removed.

Moreover, a perpetual prohibition of the importation of any product does not prevent the importation of the parasite and at the same time it will be of no profit for Phytopathological Science. It will only damage international relations if the phytopathological arguments are not scientifically founded, or if there is a one-sided arrangement. In fact, if we wish to effect an international cooperation of all phytopathologists for the control of plant diseases and research upon plant diseases, for the good of agriculture and horticulture in the whole world, we must assume the following attitude with regard to the international movement of plants and plant-products:

1. In every country all pathologists must see to the control of the diseases of the home crops as best they can. Apart from the idea of importation or exportation this is necessary in order to keep down the cost of production in behalf of the prosperity of the country. *Indirectly* this gives at the outset a sound basis for international cooperation, because the results of the investigations are published and every investigator of any nationality will gladly accept the help of results obtained by colleagues abroad. At this time, the end of this international phytopathological congress, it would be carrying coals to New-Castle to prove this by examples. *Directly* this will afford the best guarantee that the products will come up to reasonable requirements of the foreign customer.

2. If the phytopathologists in care of the protection of the home crops against the importation of foreign plant diseases should discover that any imported product contains a parasite endangering the native cultures, they must immediately acquaint their colleagues in the exporting country with this fact. The burden of proof that these dangers really exist ought to rest in the first place on those who object to the importation of the product concerned. They should show that the objectionable parasite is actually present in the product and really endangers the home crops.

If these purely phytopathological objections are sustained on scientific grounds, then the exporting country will have to remove these objections in order to prevent a temporary exclusion of her product. If it should be unable to do this immediately, it has no right to protest against the measures taken. From that time the burden of proof for the removal of the danger should rest upon the exporting country, before it might claim the canceling of the restrictions.

This means that restriction of the importation of any plant product may never take the form of a general quarantine against all plant diseases, but should be a quarantine against those plant diseases only that have been shown to be new or dangerous. A quarantine, therefore, should always be specific, local, and temporary.

I may be permitted to interpolate here some remarks relating to the very important lecture of Dr. L. R. Jones given yesterday morning. He said: "Our friends from the other side must consider that in some circumstances we need

the quarantines." I wish to emphasize, that, so far as I know nobody will deny that in some cases quarantines can be justified in so far as they are made emergency measures and that as Dr. Jones himself suggested, they should be *temporary*. If on purely scientific grounds the temporary necessity has been proved, nobody can object. But, what is the value of quarantines in phytopathological research and in the control of plant diseases?

Rightly, Dr. Jones pointed out that the quarantine measures *do not* promote the solution of the problem of the control of diseases, and just for that reason he asked that there should be granted an allowance for research along with each quarantine measure taken. This includes, in my opinion, not only the emergency measure of the restrictions, but also he takes it for granted that the restrictions should be canceled as soon as this research has led to a satisfying result.

I have already explained why the exchange of the products of agriculture and horticulture is inseparably connected with the exchange of all other commodities. We may, however, just for a moment, accept the point of view of a country for which the exportation of its products of agriculture or horticulture is a question of its very existence. Or as every country has some cultures from which it is obliged to export the overproduction to other countries, we may better try to accept for a moment the point of view of the phytopathologists located in those districts and in charge of the research and the control of diseases of the cultures concerned. Those phytopathologists have to protect their cultures and are obliged to eliminate all reasonable dangers that may exist for any customer.

What will, however, be their satisfaction, when having succeeded by very hard work in mastering innumerable difficulties, they see their products refused, products which they have made as sound as it is humanly possible to make them, and which they have to export in order to get in exchange the commodities they cannot do without? Does it seem unreasonable that they should ask a scientific basis for the refusal of their products? Can there be any international cooperation if there is no mutual confidence and no mutual appreciation of each other's work?

In the interest of sound international relations an international discussion would be desirable before any restrictive measures be taken. This would also foster phytopathological science.

Besides the discussion of special cases there are a great many general problems connected with the problem of movement of plants that only can be solved by close international cooperation. Time is too short to permit of discussing all these. I will mention only a few which bear upon my own experiments; not because they are of greater importance than any other problems, but because I think it desirable that a scientific discussion should be based on the personal experiences of the debater.

1. THE PROBLEM OF BIOLOGICAL STRAINS

This is not only of great general scientific importance, but it also bears upon the problem of international plant movement, inasmuch as we have to know if a parasite of a special crop may migrate to some other crop. My own experiments have proved that the nematodes of the Narcissus form a special strain essentially

different from the other strains I know. It is evident, therefore, that we may speak of a danger to another crop only when we have proved that the strain will migrate to that crop.

2. THE DIFFERENCE BETWEEN PRIMARY AND SECONDARY PARASITES

In my opinion the bulb mite (*Rhizoglyphus echinopus*) is only a secondary parasite. I have this opinion as a result of general experience in the bulb district, as well as from special experiments. Experiments made at the Phytopathological Laboratory at Harpenden, England, under the direction of Dr. Fryer, have had the same results.

Likewise, I am sure that the little Narcissus fly (*Eumerus strigatus*) is only a secondary parasite. My experience of nine years in bulb culture together with a great number of experiments have given me that conviction.

3. SCAVENGERS

Besides the above mentioned cases, a great number of secondary scavengers appear in every shipment of plant products through bruising of the plants or fruits or by heating in transit. The greatest care of all the phytopathologists in the world cannot possibly prevent this. As a matter of fact the occurrence of those scavengers can never form a reasonable basis for the prohibition of the importation of any plant product. This would make every interchange of plant products impossible.

Still, the cooperative study of the best conditions for shipment of plant products will be of great importance for the international movement of plants.

I am quite well aware that the exposition of the problem in this way does not at all solve the problem. However, where there is a will, there a way will be found, and it depends especially on an agreement regarding the basis on which the solution ought to be founded. I am confident that this basis may be found, because even Güssow, who has shown such clear insight respecting the difficulties of the problem, and has exposed the dangers connected with it so well, comes to the conclusion that a reasonable freedom from diseases must be the basis of the international exchange of plants and plant products. And especially in the *reasonableness* will be found the cue to clearing away the controversies.

For the expression "*reasonable* freedom from diseases" is not only a protection for the exporter, but also for the importer. The latter may appeal to this as a reasonable protection of his home crops, whereas the exporting country may claim a reasonable basis for any objections against his products.

It depends largely on the decision we may take here with regard to this problem whether in the future we shall get a searching for arguments for exclusion —seeking strength in a strong isolation—or a close international cooperation in the control and research of plant diseases, based on mutual appreciation and confidence.

The profit of human welfare as well as the profit of our international phytopathological science requires the last and I am glad to say here that the phytopathologists of the whole world greatly admire the achievements the American phytopathologists have accomplished.

INTERNATIONAL PLANT DISEASE LEGISLATION
AS IT AFFECTS THE BRITISH EMPIRE[1]

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I propose to give a very brief survey of conditions in regard to plant import regulations as they affect especially the British Empire and to discuss a few of the general principles on which such regulations are based. Conditions in England are widely different from those in many other parts of the Empire and the difficulties and responsibilities of official plant pathologists in England are much less than in the British Dominions and Colonies. The agricultural industry of England is a relatively unimportant one, compared with the other great national industries, and it is also a very varied one, not dependent on the growing of a few crops on a large scale, as is the case in some of the exporting Dominions and Colonies. There is nothing in England comparable to the rubber-growing industry of Malaya, the tea, jute, and cotton industries in India, or the cocoa industry of the Gold Coast, industries on which a great part of the national prosperity of these countries depends. The Government plant pathologist in such countries has to watch very carefully for possible dangers arising from the introduction of foreign diseases, and may have to take measures of considerable stringency in order to safeguard a very valuable industry and one which often it would be hard, or perhaps impossible, to replace. As it happens these measures do not ordinarily affect England, since most of the crops concerned are grown in the tropics and are not liable to serious danger in regard to importations from temperate zones. But, so long as these considerations have weight—and that is likely to be for a very long time—it is useless to hope to get the British Empire mycologists as a body to endorse any proposal for the abandonment of their powers to impose severe restrictions on the free circulation of living plants. The persons responsible for the safety of the Eastern rubber industry cannot agree to any proposal which would force them to admit living rubber plants from South America and the Caribbean, plants which might bring in the Hevea leaf disease that has prevented the establishment of a plantation rubber industry in those regions. Not only would the mycologists oppose any such suggestion, but the whole rubber industry would be up in arms at once and could prevent the Governments concerned from agreeing. I mention such a case merely to show that no general proposals, on the lines of those of the Rome Convention of 1914, that might make it obligatory to admit living plants even though these be certified free from disease, have any chance of being accepted in the Empire as a whole. Certain total prohibitions will remain in force.

Apart from these cases in the tropical Dependencies, which are not as a rule serious impediments to trade and only affect England slightly, there are numerous quarantines and restrictions on plant imports in the temperate Dominions, States, and Colonies. They are based on certain biological facts and principles regarding which there is room for much more information than we possess at present. Both in the British Empire and in the United States the necessity of distinguishing between two types of dissemination, at least as regards fungi and bacteria, is being more and more recognized. There is the problem of dissemination of a parasite within a continuous land area, whether the area is divided up by political boundaries or not, and there is that of discontinuous dissemination, mostly between areas separated from one another by the ocean.

In regard to the former of these, most pests of long standing have already reached all parts of the continuous land area in which they can maintain a footing, and restrictive measures are generally confined to newly-introduced pests which have come from other parts of the world. We do that in England. We do not impose restrictions as a rule in the case of diseases of long standing, since these have reached all parts of the country, but diseases like wart disease of potatoes are subject to quite different treatment. So in the United States and Canada it is chiefly the new diseases that are responsible for internal restrictive legislative measures.

The prevention of the introduction of exotic pests from a distance, mainly from overseas, is a very different matter. Here much exact knowledge is required and is not always readily available. With fungous diseases one has to have clearly in mind the crop which one wishes to protect and then to examine what pests it suffers from in other parts of the world that might be destructive if introduced. Unfortunately one has often to go further and consider what parasites of other plants, be they related to the crop one desires to protect or not, might prove dangerous if introduced. Then one has to consider the powers as a traveller of these parasites. Here we have a point which has been very critically examined of recent years. In 1914–15 I examined the question[2] in the light of the known facts of the spread of a large number of plant diseases whose history could be traced, and came to the conclusion that the powers of long distance dissemination of the parasites had been frequently exaggerated. In most cases spread along trade routes could be clearly traced and spread by natural means without human agency could not. A few years ago Orton and Beattie[3] of the Federal Horticultural Board in the United States stated that no case of long-distance transfer of plant disease by wind had been demonstrated, and that carriage of disease in ballast, except where soil was concerned, could not be definitely traced. In most of the overseas parts of the Empire it is this long distance or discontinuous dissemination that is important. The most frequent agent in such dis-

[2] Butler, E. J. The dissemination of parasitic fungi and international legislation. Mem. Dept. Agric. India. Bot. Ser. 9(1): 1917.

[3] Orton, W. A., and Beattie, R. K. The biological basis of foreign plant quarantines. Phytopathology 13: 295–306. 1923.

semination is man, and the outstanding medium of transfer is living plant material.

That is why the countries that import living plants watch their ports and intercept diseased plants or prevent their arrival.

In examining the steps taken by importing countries we might enquire; (1) are they based on sound biological data; (2) do they secure the objects aimed at; (3) do they go beyond what is necessary or expedient in securing these objects?

In regard to the first of these questions I do not propose to delay. I regard it as fully proven and abundantly illustrated by terrible examples that the main danger from exotic plant parasites lies in the readiness with which they can be introduced on living plant material, while excepting for this method of introduction there is little risk to be feared from them.

With regard to the second point, the adequacy of the measures taken to keep out exotic parasites, this of course varies from country to country as the measures taken, themselves, do. Wart disease of potatoes has been successfully kept out of many parts of the world and it is interesting to note that the first case of this disease in South Africa was brought in before the introduction of legislative measures to exclude it, though not discovered for a number of years. I believe that every part of the British Empire is satisfied that it has, in fact, kept out certain dangerous diseases by taking the necessary precautions, diseases which in the absence of any precautions would have come in.[4]

The answer to the third question, which chiefly affects plant-exporting countries like England, namely, whether the measures taken go beyond what is necessary or expedient to secure the objects aimed at, is not so easy. One finds in some countries a long list of plant diseases to be excluded, in some a shorter list of specified diseases, but, in addition, a regulation prohibiting in general terms the introduction of any diseased plant or of certain categories of plants, for example, nursery stock. It is probable that no plant pathologist would care to certify any consignment of plants as being free from all diseases, whatsoever. If, therefore, such a measure as that in Section II of the Canadian Act, which reads "No pest or disease or plant infested with any pest or disease shall be admitted into Canada," is intended to be taken literally, it would mean practical prohibition. But if it is intended merely to give power to reject any obviously diseased consignment, even when the disease present is one not specially listed, then no objection can be taken to it. Such a general clause might then even help in keeping the specially listed diseases down to a limited number, and actually assist the careful exporter in gaining admission for his consignments.

In countries which list a large number of specified diseases one finds included in this number, sometimes, diseases that are already known to occur in the importing country. I think great care is required in handling the regulations restricting the entry of these. It is, I think, quite right that consignments with a high percentage of disease should be refused, even if the disease be one already

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[4] We need only to compare the spread of potato blight with that of wart disease within the British Empire to be convinced of this.

present in the country, but this ought not to apply to consignments containing a few odd cases. To refuse 100,000 rose grafts because 20 or 30 have crown gall—when crown gall is already widely present throughout the country—is indefensible. In the report of a committee of the American Society of Horticultural Science on crown gall inspection, published a few years ago,[5] it is stated that the Committee regards as unjustifiable the rejection of an entire shipment on account of a slight incidence of this disease. What I would like to see in similar cases is the exclusion of crown gall altogether from the listed diseases, and the application of some general section which would allow the inspector to reject an obviously badly galled consignment.

In general, one would like to see the number of kinds of plants prohibited on account of specified diseases kept down to a few really important or dangerous things. I admit that it may be hard to know where to draw the line in continental areas like Australia and Canada. Still Canada has only listed specifically for fungous and bacterial diseases nine kinds of plants, namely potatoes, five-leaved pines, chestnuts, *Ribes*, *Rhamnus*, Barberry, three kinds of coniferous trees liable to attack by *Phomopsis pseudotsugae*, peaches from certain parts of the United States, and *Corylus* also from certain parts of the States. This is quite a limited list, though of course there are special regulations governing the importation of nursery stock. But even in the above list there would seem to be some anomalies. In the regulations against potatoes—directed largely against wart-disease—one notices that potatoes from Europe are refused admission altogether while potatoes from the wart-infested districts of Pennsylvania, West Virginia, and Maryland are allowed in if provided with a certificate that they were grown outside the infected and quarantined area and have been examined and found free from wart disease. A similar, and I am sure equally reliable, certificate could be given in England, and some explanation seems called for. I cannot help feeling that the differential treatment in a case like this is due to an old distrust of the phytopathological service in England, a feeling which, however justified in the past, has now ceased to have any basis in fact. One of the main advantages of conferences such as this is that the people responsible for framing and carrying out these regulations are brought into touch with one another and mutual confidence is engendered. Everything hinges on the development of confidence in the reliability of the inspection service in the exporting country and, of course, unless the service is kept at a high pitch of efficiency there can be no real confidence. I am quite sure that as long as it is possible for a country to send out heavily diseased consignments, no matter what the plant or what the disease, so long will it be impossible to get importing countries to relax their restrictions. There are signs that the importance of growing clean and healthy stock for propagation is more fully recognized than it used to be. The potato seed certification movement is a proof of that.

The position at present in the overseas parts of the British Empire is somewhat as follows.

[5] Dorsey, M. J. Symposium on crown gall inspection. Proc. Amer. Soc. Hort. Sci. **1923**: 255–256. 1924.

In many countries prohibitions are in force to the effect that no plants of particular species may be introduced from any part of the world or from certain areas, as the case may be. Such prohibitions are likely to remain, but the instance quoted in regard to the Canadian potato regulations shows that they require examination from time to time to see whether they make distinctions not justified by the facts.

In many countries all plants or certain large categories of plants, for instance all nursery stock, can only be imported under permit and accompanied by health certificates, being subject to re-inspection on arrival. No one can properly object to these requirements, provided the inspection on arrival is properly and reasonably carried out. Most of the trouble has arisen on this point. The inspectors are only human and if they find consignments coming in that should not have been sent they are liable to get stricter and stricter in regard to the country sending such consignments. It is necessary, therefore, to do everything possible in the exporting country to prevent diseased consignments being sent and unreasonable to expect any relaxation of the strictness of the inspection in the importing country until the exporting one has set its house in order.

It is, I think, quite possible that restrictive measures against the entry of living plants have reached their maximum severity, as far as concerns imports from England and other countries that have taken steps to improve the cleanliness of export consignments. I believe we may reasonably hope to see the severity of these measures gradually relaxed, as confidence in the British inspection service grows. In other words, one may be permitted to hope that, while every importing country will still prohibit certain things, the list of these will be a small one; and that, though powers will still be held to reject obviously diseased consignments, these will be severely applied only against certain major diseases not already present in the importing country while, as regards the rest, good stock will be admitted even if it includes an occasional parasite.

ORGANISATION INTERNATIONALE DE LA LUTTE CONTRE LES MALADIES DES PLANTES ET SA REALISATION PRATIQUE[1]

ET. FOEX

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The result of the formal program of the International Convention of Phytopathologists in Rome, 1912, has been the object of numerous criticisms and a cause of considerable discussion.

Deeming that an agreement of this kind is realized only when there is' no conflict with the laws of nature, Dr. E. J. Butler examined the conditions which determine the dispersion and dissemination of vegetable diseases. Although the possibility of the scattering of spores by means of wind, water, and birds are evident, it seems that these mechanisms play a part only in continuous, not in discontinuous dispersion. We appreciate what Orton and Beattie saw, that is, a continent as a closed world, in which the dynamic equilibrium occurs between the animal or plant species which people it. According to these authors any introduction of a new organism which is specifically different from those which are already there tends to upset the balance and to cause disturbances. Often a parasite will be less disastrous in a country where it is indigenous than in a country where it has been introduced. These ideas are expressed by Orton, Beattie, and Güssow, who deplore that the delegates to the International Phytopathological Convention of 1914 have not realized that there are intracontinental phytopathological problems as well as intercontinental.

We admit that man is responsible, on the whole, for the introduction of plant diseases and that parasites are imported especially with their plant hosts. Moreover, plant products destined for the manufacturers' use appear to us as an important factor in the introduction of the parasite. Furthermore, do we know what will be the ultimate utilization of the plant parts imported? The appearance of an exotic parasite, although never desirable, is not necessarily any more disastrous than of indigenous ones. Certain of the latter cause great ravages (for example, rusts, "foot rot" of cereals). Does a parasite lose its virulence progressively, does its host become adapted to it progressively? We do not know. In any case, most fungi introduced long ago (*Phytopthora infestans*, *Uncinula necator*, *Plasmopara viticola*) always appear to be equally disastrous.

Since the dynamic equilibrium which is upset by the introduction of a new parasite tends finally to reestablish itself, there is no doubt that this process is

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[1] Presented before the International Congress of Plant Sciences, Section of Pathology, Ithaca, New York, Aug. 20, 1926.

Editor's Note: It is much to be regretted that space requirement has necessitated the substitution of an abstract for the full paper sent by the author to be read at the Congress.

extremely slow. However that may be, it is essential to enforce laws against the introduction of foreign parasites.

Will an international phytopathological regulation be realized and will it be efficacious? In any case, when we proceed to its elaboration, we should not forget that it comprises two sides: (1) one that perhaps only technicians can consider (entomologists, phytopathologists); (2) another that can be usefully studied by the economists and jurists alone. An international phytopathological agreement can be realized only if it is very simple, of a general nature, of a character satisfactory to the lawful claims and demands of all countries. It is in this spirit that the following conclusions which Mr. Saulier and ourselves presented at the International Agricultural Congress of Varsovie in 1925 have been drawn up:

Inspired by the principles already expressed, we have the honor to submit the following resolutions for the approbation of the Congress:

The International Agricultural Congress recognizes the great importance indeed even the necessity, for an international entente, aiming:

a. To assure the protection of agricultural products against plant and animal parasites.

b. To guarantee each country against the introduction of dangerous parasites coming from foreign countries.

The International Agricultural Congress published the following resolutions:

1. That the new Phytopathological Conference, in relation to an international convention for plant protection, take place during the year 1926.

2. That the program of the conference be arranged by specialists (phytopathologists, entomologists, economists, jurists), and that it should be based upon the following:

a. The final act of the Pathological Conference of 1914.

b. The criticisms to which this act has been subjected in different countries.

c. The phytopathological legislation in various countries.

3. That the program be established on a basis acceptable to all states.

4. That in all states a uniform measure should be enforced to assure crop protection. Each country should possess:

a. A duly organized governmental service for crop protection and defense.

b. Sufficiently numerous entomological and plant pathological experiment stations well provided with personnel and equipment.

5. That the program of the Conference be communicated to the various states six months before the meeting.

THE VALUE AND LIMITATIONS OF HISTOLOGY
IN VEGETABLE TAXONOMY

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The study of the internal structure of vegetative organs has been comparatively little resorted to as a basis of, or an aid in, classification. In Europe much has been done in the way of supplementing descriptions of families or smaller groups by more or less extensive descriptions of internal structure, but American botanists have not gone so far, nor have they made any considerable use of these characters in the practical determination of plants. Most American taxonomists deny, or at least doubt, the correctness of conclusions regarding relationships that may be reached on this basis, while practically all of them deny the necessity or the great utility of such methods.

On the other hand, there is an increasing number who claim that the general use of anatomical methods would prove of great assistance and would increase the accuracy of classification, when used in connection with ordinary methods. Some go so far as to claim that a complete histological system of classification and diagnosis is not only practicable, but would be more accurate, scientifically, than the system now in use. They are accustomed to speak of our taxonomists, as a class, as being "old fashioned" because of their adherence to the present system. This group of comparative anatomists, as we may call them, is becoming so large, and their activity is so great, that the questions involved are certain to become the subject of much controversy, so it has seemed desirable, on this occasion, to consider the present status of the subject.

It may be regarded as an established and accepted fact that the critical anatomical examination of timbers, fibers, foods, drugs, and similar useful plant products in economic work is an absolute necessity. In these examinations, the object sought is merely to determine the identity, purity, or quality of the particular article under examination; or, perhaps, to furnish a description that may serve to guide others in such identification. The work is performed in the interest of economics and is not necessarily of scientific interest. Nevertheless, the fact that its findings are trustworthy, and capable of deciding correctly important commercial questions, is significant of important possible scientific application. In none of these cases is a broad study of comparative structure required, but there are other fields of botanical work in which such comparative study is of great importance.

No botanical collector in new or little known territory has returned without being laden with materials that are indeterminable, because wanting in the flower or fruit material that is indispensable in classification and determination by ordinary methods. Even when such material is present, the specialist very

frequently returns the specimens unidentified, because they are not in the proper stage of development to supply the necessary data. Especially have I found this true of valuable timber trees. Not only my own collections, but those of others sent to me for determination have invariably comprised large fascicles of specimens bearing only leaves, with collection data and frequently local names, indicating valuable structural properties and sometimes important uses, but quite indeterminable for the reasons mentioned. Local names are usually of little service and are often actually misleading, because the same tree often has various names in different localities, and not infrequently the same name is elsewhere applied to a different tree. Often indeed, we are without the slight assistance that the leaves might contribute, the specimens comprising mere fragments of the wood, with or without the bark. The number of such specimens now lying in American museums and herbaria doubtless runs into scores, if not hundreds.

Even greater are the difficulties connected with the identification of aboriginal drug materials. It is the rule, rather than the exception, for new drugs to appear in commerce without the material that is required for their botanical identification. Quite frequently the genus, or even the family cannot be determined. We are all acquainted with drugs that have been important articles of commerce for many years before anything was known of the plants yielding them. When these plants are themselves unknown to science, there is no remedy, but in many cases they are known, though we have not the necessary knowledge to enable us to connect the drug material with its botanical source. Had the original description of the species included an account of its internal anatomy, such identification might be possible. Or, had the internal structure of the genus or even the family been sufficiently well-known, we might be enabled to go a long way toward its determination. There have been many cases in which mistakes from such failure have resulted in heavy financial losses and sometimes in far more serious consequences. The long-continued substitution of *Cannella alba* for Winter's bark, has extended its results beyond commercial designation and has left a permanent impress on botanical nomenclature. Coto bark was generally employed for several decades before its botanical identity was more than guessed at. The old-world cinnamons were indefinitely known for a century, and our knowledge of the source of South American cinnamon was still more meagre. In India, the British government wasted millions of pounds sterling in the cultivation of the worthless *Cinchona Josephiana*, in the belief that it was a true variety of *C. calisaya*. Had its bark been examined by modern pharmacognostical methods, this mistake would have been impossible. A volume might be filled with histories of exploitation, erroneous or intentional, made possible by the indefinite information that accompanied the introduction of the articles. It is not always possible, even in the case of mature edible fruits, to make a positive determination of genus or family. Were all such materials to come to us with complete representation of flowers and fruits, instances of their doubtful classification would be rare.

With this ever-increasing evidence before us of the insufficiency of anthology,

carpology, and gross external characters, in enabling us to deal with fragmentary materials, the demand for supplementary or substitute methods of classification or description has become strong and insistent. It is obvious that with the possession of a comparative key to tissue-structure, similar to that in use for flower and fruit-structure, we might with certainty, though not so easily, determine most of our imperfect specimens of unknown plants.

The claim that histological diagnosis would be of service in securing greater accuracy in determining and classifying plants is worthy of the most careful attention. The records of economic botany are filled with instances in which the determinations of systematic botanists have been found useless when one or more species of a genus have been found to possess useful properties. As in the cases of *Cinchona, Erythroxylon, Rhamnus*, and *Rheum*, the useful properties may reside only or chiefly in certain species, the others being useless. In such cases it has almost always been found that the existing descriptions are too faulty to supply accurate and positive identification, and economic botanists have been obliged to revise the literature. In these cases, histological study has always been found indispensable. But we need not wait for the economic botanist to uncover defects in classification. We have only to compare the treatment of many genera by different authors to see what great difficulties of opinion exist among them. It is, of course, possible that in some cases the introduction of histological evidence might increase the existing confusion, but it is certain that in many others it would enable us to settle points in dispute. In any case, it cannot be regarded as erroneous to secure the fullest possible evidence.

The use of cellular characters for identification was first applied to the study of trichomes, as distinguished from the general indumentum-characters resulting from them. Employed at first merely in the identification of species, it was soon found that these trichomes exhibited group characters that distinguished genera and even families, and which might be used as an auxiliary in general classification. Probably the earliest American contribution on this subject was by Charles F. Cox, then President of the New York Microscopical Society, which dealt with the family characteristics of trichomes. The application of microscopical methods in the examination of internal structure in the identification of fibers, timbers, and drugs was found from the beginning to be efficient, but the establishment of general confidence in it was difficult, this distrust being almost wholly the result of ignorance of the facts, and want of familiarity with the methods, but in spite of distrust and opposition, this method of identification has become perfectly established. In pharmacognosy, it has been found quite reliable, even when the substance under examination is in the form of a fine powder, and these methods are now regarded as dependable as those based on characters of flower and fruit. It soon became evident, moreover, that analytical keys could be constructed that would provide for the classification of more or less extensive groups of materials.

Under such conditions, it was inevitable that there should arise a suggestion as to the possibility of constructing a complete key to the groups and species of the vegetable kingdom, based wholly upon internal structural characters. By those whose knowledge of plant structure was confined chiefly to the reproduc-

tive organs, the suggestion was received with incredulity, and mostly with derision. No other reception should or could have been anticipated, and it was shared by many well-informed histologists. This doubt and disbelief followed two quite distinct lines. One related to the existence of characters extending through the recognized groups;—classes, orders, families and genera, sufficient to distinguish them. The other, assuming that such characteristics did exist, questioned whether their occurrence in the plants would run parallel with the similarities and differences in reproductive characters, which form the basis of our present classification. If not, then which system would result in the more natural classification? There is ample evidence that, in general, our present classification indicates genetic relationship, the only scientific objective of taxonomy. Would a classification based on internal anatomy do the same? If it were found that two groups now associated exhibited anatomical differences which would assign them to different positions in the series, which would be the more likely to indicate their phylogeny? Would the antiquity of a common anatomical character coincide with that of the presently accepted reproductive character? The reflection of genetic origin in the reproductive characters now used in taxonomy is so obvious, and the classification based upon the latter so simple and in general so satisfactory, that there should be great hesitation in accepting any proposition to displace it. Our present system provides for the ready valuation of both great and small characters of all groups, and, in connection with external vegetative characters, enables us to separate all forms, even inconstant variations. Taxonomists, therefore, in the light of present knowledge, are doubtless correct in the opinion that no other system will ever displace the present one, as to its fundamentals.

A more important question, and a less doubtful one, is whether a series of anatomical characters can be found that will conform to our present classification, and enable us to assign plants in it by an examination of their internal structure, in the absence of reproductive organs.

Applying this question to particular cases, we note that in the family Gesneriaceae we distinguish two genera, because one possesses a disk of five distinct and equal ligules, while in the other two of these ligules are smaller and coherent. Within one of these genera we distinguish two species by the relative lengths of disk and ovary. These differences, however small, are clear and constant. If one species possesses medicinal value, or is of use in coloring or tanning, the substitution of the other may be quite inadmissible. The employment of these characters in taxonomy is therefore not only necessary in economics but sound from the genetic standpoint. Who would expect that such a slight difference in the development of an appendage to the torus would be accompanied, necessarily or usually, by diagnostic characters in internal structure? In the Apocynaceae, we classify on the basis of very similar variations in the same organ or in a substigmatic appendage; in the Meliaceae and Amarantaceae by similar differences in the stamen-tube and anthers. In the Asclepiadaceae, it is the endless variations in the attachment and character of the crown that afford our characters. Assuming that there are associated anatomical characters in one of these families, does it follow that a similar difference would accompany the same floral differ-

ence in the other? We may, of course, be met by a counter-question as to whether we might not find more reliable characters in internal structure, and thus be enabled to discover a more natural relationship. We must, in fairness, acknowledge that such cases have occurred, and we must unquestionably recognize the value of the anatomical method as an aid in reaching a correct conclusion. There are many questions regarding relationship that hitherto have baffled taxonomists, and it is not too much to hope that histology may yet determine them. Certain it is that two species can be distinguished in most cases, by anatomical examination. It is by no means so certain that a character can be found that will apply to all the species of a genus and be absent in related genera. So far as my own experience goes, I may formulate my conclusion by saying that positive histologic evidence is reliable, but negative evidence may not be. If we find that two plants which taxonomists would regard as identical are anatomically different, they should be regarded as two, but if taxonomists find them different, they must not be united because anatomical differences are absent. This is on the axiomatic ground that two things which are different are not the same.

The present stage of this subject may be described by saying that our evidence is not sufficient to justify a decision. Studying Solereder's monumental work, one is equally impressed by the great extent of the ground that he has covered, and by the number and size of the missing parts. The indications for future contributions are in the direction of a great number of independent studies of groups, proceeding from the smaller to the larger. Determining all the characters and the distinctions of all the species of a genus may enable us to determine which of such characters pertain to the entire group. Proceeding with those of the other genera of the family, we may determine which generic characters apply to all the genera of the family. The work is enormous and will require an army of investigators. Who is to perform it? It is almost too much to expect that taxonomists will forsake their own exacting duties to engage in it on an extensive scale.

My reason for presenting this subject to a body of pharmacognosists is my belief that this work falls largely within their province. They can hardly be expected to seek broad generalizations, but they can easily and naturally place on record a vast amount of evidence that can be useful to those who engage in comparative studies. The methods pursued in pharmacognosy are precisely those on which the solution of this problem depends. Moreover, a pharmacognostic problem almost necessarily involves some degree of comparison and the recording of diagnostic characters. A moderate degree of extension of the field of observation would raise the plane of an economic to that of a genuine scientific standing. There is, at the present time, much talk in pharmaceutical circles on the subject of research work; an amount that is by no means justified by present results. Here is work that is most closely related with their professional activities and that may be of the greatest service in solving the problems of plant evolution. If accompanied by comparative study of plant chemistry, its performance would reflect high credit on the pharmaceutical profession, and do more to distract attention from the absurd criticisms now directed against it because of commercial offenses, than anything of which this writer can conceive.

THE NEED OF A MORE THOROUGH ANATOMICAL INVESTIGATION OF DRUGS[1]

ABSTRACT

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The circumstance that at present drugs seldom come to the hand of the pharmacist in the whole condition, but mostly in fragments or reduced to powder, requires a more exact investigation of their identity and purity than was necessary in earlier years. We consider the characteristic anatomical features of the drug a basis for such an investigation. With a single figure of a cross section, such as commonly given in textbooks, very little is accomplished in many cases.

It is not only necessary to investigate official drugs in their different developmental stages, and to include the results in the accounts given in pharmacopeias, but the latter should also refer to the anatomical characteristics of the commonest substitutes and adulterants. An exact anatomical investigation of those adulterants has heretofore been assigned too little importance, since the practical pharmacist, even if he consults a good literature, finds either no statements or something which after long search is of little use. The anatomical investigation should in the future be extended not only to officinal drugs, but to all which have pharmaceutical uses or serve as adulterants. It is necessary to go more deeply into anatomy than is at present customary, paying attention to small differences which are not at once evident. Then it is possible, as a number of works in our institute have shown, to set up clear differences and characters of identification for closely related species. The roots, barks, leaves or seeds of a family are rather sharply characterized anatomically, and the data permit easy identification in a key based on these anatomical characters. With such a key at hand it becomes easy for the practical pharmacist to establish the purity of a drug and to detect adulteration.

In the pharamaceutical establishment at Basel we have undertaken such studies with good results and have made identification tables for the following drugs: Umbelliferae fruits, Cinnamomum barks, Cupressineae leaves, Compositae leaves, Labiatae leaves, Iridaceae leaves, palm seeds, Myrtaceae barks, Umbelliferae roots. When all of these results are later brought together in a large tabular reference work, the investigator and the practical pharmacist will have at hand an invaluable aid. Only if different institutions cooperate will the undertaking be wholly successful.

The anatomy of drugs, which many botanists think settled, shows tself to us in each new work as a field in which much of importance remains to be done.

[1] Presented in abstract form before the International Congress of Plant Sciences, Section of Pharmacognosy and Pharmaceutical Botany, Ithaca, New York, Aug. 17, 1926. [Read by the sectional Secretary, Heber W. Younghen.]

ÜBER ENTSTEHUNG UND FUNKTION DER ÖLDRÜSEN BEI LABIATEN UND COMPOSITEN[1]

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Obgleich man meinen sollte, dass die Öldrüsen der Labiaten und Compositen in der langen seit ihrer Entdeckung verstrichenen Zeit genügend erforscht seien, haben einige Beobachtungen mich zu Ergebnissen und Folgerungen geführt, die von den bisher in der Literatur niedergelegten Ansichten abweichen und mir der Mitteilung wert erscheinen.

Gewöhnlich wird angenommen, dass die das ätherische Öl sezernierenden Zellen, das Epithel, die bei den Labiaten durch Längsteilung, bei den Compositen durch Längs- und Querteilung der Endzelle eines kurzen Haares entstehen, das Öl durch die Zellwand hindurch abscheiden, ferner dass das Öl die die Zellwand überziehende Cuticula nicht zu passieren vermag und sich infolgedessen unter derselben ansammelt, sodass die Cuticula von der Zellwand abgehoben wird und eine grosse Blase über dem Epithel bildet. Die Folgerung aus diesen Sätzen wäre, dass die Cuticula stark gedehnt wäre und dass das Öl in der Cuticularblase unter einem sehr hohen Drucke stehen müsste.

Tschirch ist der Meinung, dass das Öl nicht in den Zellen des Epithels entsteht, sondern dass diese Zellen nur Stoffe enthalten und erzeugen und nach aussen abscheiden, die man elaiogene Stoffe nennen könnte, die erst beim Passieren der Zellwand in Öl umgewandelt werden. Er glaubt nachgewiesen zu haben, dass die Zellwände des Epithels nicht aus 2 Schichten (Cellulosewand und Cuticula), sondern aus 3 Schichten bestehen. Zwischen Cellulosewand und Cuticula soll sich noch eine schleimige Schicht befinden, die Tschirch die "resinogene Schicht" nennt, und die aus den äusseren Teilen der Cellulosewand entstehen soll. Tschirch stellt sich vor, dass die elaiogenen Stoffe, die vom Epithel abgeschieden werden, die Cellulosewand passieren können, in der resinogenen Schicht dann in Öl umgewandelt werden und nun als Öltröpfchen nicht wieder durch die Cellulosewand in die Epithelzellen zurückwandern können. Die Umwandlung der elaiogenen Stoffe in Öl kann auf die Einwirkung von oxydierenden, reduzierenden oder spaltenden Enzymen zurückgeführt werden. Auch wenn man diese Anschauungen von Tschirch für richtig hält, ergibt sich als Folgerung aus ihnen, dass das Öl in der Cuticularblase unter hohem Drucke stehen muss. Haberlandt spricht dies auch deutlich aus, er sagt, dass in der Blase ein hoher Druck herrscht und dass die Blase stark gedehnt ist.

Es ist mir nun in einigen Fällen gelungen, die Blase durch eine Nadel oder das Messer zu verletzen, ohne dass das Öl herausgespritzt wäre. In diesen Fällen

kann das Öl also nicht einen hohen Druck in der Blase gehabt haben. Ich sehe nur 2 Möglichkeiten, diesen Befund zu erklären:

(1) Entweder nimmt die Cuticularblase während der Produktion des ätherischen Öles *durch Wachstum* an Grösse zu—

(2) Oder das Epithel nimmt während der Produktion des Öles an Grösse ab, und es schafft durch diese Verkleinerung den Raum, den das produzierte Öl einnimmt.

Die Entscheidung, welche von beiden Möglichkeiten vorliegt, konnte durch Grössenmessungen getroffen werden. Es zeigte sich, dass sich die Compositen und die Labiaten verschieden verhalten. Bei den Compositen ist die mit Öl vollständig gefüllte Ölblase nicht grösser als die ganz junge Drüse, die noch kein Öl produziert hat, die Epithelzellen sind aber wesentlich kleiner, manchmal kaum noch zu erkennern. Bei den Labiaten ist die mit Öl gefüllte Drüse immer erheblich grösser als die junge, noch ölfreie Drüse; bei den Labiaten muss also ein Wachstum der Cuticula erfolgen. Die weiteren genauen Untersuchungen hat Herr Klug in meinem Laboratorium unter meiner Aufsicht durchgeführt; sie haben folgendes ergeben.

Compositae. Die Drüsen entstehen dadurch, dass eine Protodermzelle über das Niveau der angrenzenden Zellen hinauswächst und sich der Länge nach teilt, die beiden Tochterzellen dann mehrere Querteilungen durchmachen. Die junge Drüse stellt dann eine aufrecht stehende, meist aus 6 bis 8 Zellen bestehende, etwa herzförmige Zellscheibe dar, die von der Cuticula überzogen ist (Abb. 1). Ihre Zellen haben reichlichen Protoplasmainhalt, wohl ausgebildete Zellkerne und deutliche Zellmembranen. Noch vor Beginn der Ölbildung aber werden die Membranen undeutlich und die Zellkerne desorganisiert. Infolge des Schwindens der Zellwände fliessen manchmal die Protoplasten zu einer einheitlichen Masse zusammen, sehr häufig bleiben sie trotz des Fehlens der Membranen getrennt. Die Zellkerne lösen sich gewissermassen im Protoplasma auf: färbt man die Schnitte durch ganz junge Drüsenanlagen mit Eisenalaun-Haematoxylin, so zeigen sie stark gefärbte, scharf begrenzte Zellkerne in fast farblosem Plasma, je weiter aber die Desorganisation der Zellen fortschreitet, desto unschärfer werden die Umrisse der Kerne und desto dunkler färbt sich das Plasma, und schliesslich ist oft die ganze Kernsubstanz diffus im Plasma verteilt. Die Desorganisation der Zellen beginnt meist im obersten Zellenpaar, seltener in den tiefer gelegenen Zellen (Abb. 2). Erst nach Beginn der Desorganisation beginnt die Ölbildung, und je mehr Öl produziert wird, desto mehr sinken die Zellen zusammen (Abb. 3). Diese Vorgänge erinnern sehr an das Verhalten der lysigenen Öldrüsen der Rutaceae, bei denen ja auch die Ölbildung von einer Zelldesorganisation begleitet ist. Ja ich glaube, dass die Analogie noch weiter geht. Schon Haberlandt hat beobachtet, und ich habe es später bestätigt, dass es bei den Rutaceen nur ein kleiner, schon in den jüngsten Anlagen kenntlicher Komplex von Zellen ist, der einer "lysigenen" Desorganisation anheimfällt. Bei der weiteren Grössenzunahme der Rutaceendrüsen werden angrenzende Zellen nicht mehr aufgelöst, sondern wir müssen annehmen, dass bei dem Wachstum des Organs, in dem sich die Drüse befindet (Blatt z.B.), das wachsende Gewebe

elaiogene Stoffe an die Drüse abgibt, die in der aus den desorganisierten Zellen entstandenen Masse in Öl umgewandelt werden, sodass wir diese Masse mit Recht als eine aus Zellen entstandene resinogene Schicht, d. h. als das Laboratorium bezeichnen dürfen, in dem die Pflanze die letzten Reaktionen der Ölsynthese vornimmt. Nach dieser Auffassung wären also die elaiogenen Stoffe Abfälle und Nebenprodukte des Stoffwechsels der normalen Zellen, und sie können als das eigentliche und primäre Sekret dieser Zellen betrachtet werden. Sie werden von den normalen Zellen an die Drüse abgegeben, die sie durch Umwandlung in Öl, d.h. in einen in Wasser und Zellsaft unlöslichen Stoff, unschädlich macht, der eben infolge seiner Unlöslichkeit nicht mehr in die normalen lebenden Zellen zurückkehren kann. Ganz Ähnliches nehme ich bei den Drüsen der Compositen an. Wenn die Zellen der Drüse desorganisiert sind, werden die in ihnen schon enthaltenen elaiogenen Stoffe in Öl verwandelt, neue Mengen von elaiogenen Stoffen werden ihnen zugeführt und wiederum in Öl verwandelt, bis die Drüse schliesslich fast ganz mit Öl gefüllt ist. Die Zufuhr der elaiogenen Stoffe erfolgt offenbar in wässeriger Lösung, das Wasser, das als Transportmittel diente, wird entweder von den normalen Zellen wieder aufgenommen oder es verdunstet durch die Cuticula hindurch. Die durch Desorganisation der Drüsenzellen entstehende Masse ist also auch bei den Compositen das Laboratorium, in dem die Pflanze die letzten Reaktionen der Ölsynthese, die Umwandlung der elaiogenen Stoffe in Öl vornimmt, und die elaiogenen Stoffe sind als das primäre Sekret der lebenden Blattzellen zu betrachten. In Übereinstimmung mit dieser Auffassung haben wir in keinem Falle die nach Tschirch zwischen Cellulosewand und Cuticula befindliche Schleimschicht (resinogene Schicht nach Tschirch) auffinden können. Vielmehr ist nach unserer Meinung eine Cellulosemembran überhaupt nicht mehr oder nur in kleinen Resten vorhanden und eine resinogene *Wand*-schicht nicht nötig, weil die ganzen Zellen "resinogen" geworden sind. Sehr merkwürdig ist, dass noch vor Beginn der Ölbildung die Drüse gegen das Blattgewebe durch Einlagerung einer wahrscheinlich cutinisierten Lamelle in die Basalwand abgeschlossen wird. Bekanntlich sind cutinisierte Membranen durchlässig für Wasser, nicht aber für Öle. Die Cutinisierung gestattet also den Eintritt der elaiogenen Stoffe in die Drüse, verhindert aber die Zurückwanderung des Öles in das Blattgewebe.

Labiatae. Die Drüsen entstehen dadurch, dass eine Protodermzelle sich über das Niveau der angrenzenden Zellen erhebt und 2 Querteilungen durchmacht. Die eine Querwand liegt im Niveau der Aussenwände der benachbarten Epidermiszellen, die andere ein wenig höher. Die Endzelle des so entstehenden dreizelligen Haares schwillt an zu kugeliger oder ellipsoidischer Gestalt. Selten (*Pogostemon*) bleibt sie ungeteilt, meist teilt sie sich durch in bestimmter Anordnung und Reihenfolge auftretende Wände in 4, 8 oder 12 Zellen, und zwar ist die Richtung dieser Wände immer senkrecht zur Fläche der Epidermis, Querteilungen der Zellen kommen m.W. nicht vor. Das so entstehende Köpfchen hat reichlich Plasma, zarte, aber deutliche Zellwände und deutliche Zellkerne. Es ist von der eng anliegenden Cuticula überzogen (Abb. 4). Im nächstälteren Stadium aber hat die Cuticula eine erhebliche Vergrösserung erfahren und bildet infolgedessen

eine den Scheitel des Köpfchens umlaufende, grosse Falte. Man gewinnt den
Eindruck, als ob es besonders die seitlichen Wandteile des Köpfchens wären, an
denen grössere Mengen von Cuticularsubstanz gebildet würden, und als ob nun
die schon vorhandene Cuticularhaut nach oben, gegen den Scheitel des
Köpfchens geschoben würde, wo es dann schliesslich zur Aufrichtung einer grossen
Falte kommt. Sobald die Falte fertig ist, beginnen die Köpfchenzellen ebenfalls
wieder zu desorganisieren; ihre Zellwände, besonders aber ihre Zellkerne werden
in gleicher Weise wie bei den Compositen undeutlich, das Plasma, das die Kern-
substanz aufnimmt, wird immer stärker färbbar. Auch hier bleiben oft trotz des
Schwundes der Zellwände die Zellgrenzen sichtbar, weil die Protoplasten der
Zellen nicht zusammenfliessen (Abb. 5). Erst nach Beginn der Desorganisation
beginnt die Ölbildung, und indem nun die grosse Falte der Cuticula verschwindet
und sich glättet, entsteht ein Raum, in dem das Öl sich sammelt, der viel grösser
ist als es die junge Drüse war. Dieser Ölraum erfährt eine weitere Vergrösserung
noch durch das Kleinerwerden und Zusammensinken der Epithelzellen, und
zwar sind es, wenn 12 Epithelzellen vorhanden sind, die mittleren 4 Zellen, die
die stärkste Verkleinerung zeigen. Auch bei den Labiaten wird die Drüse noch
vor Beginn der Ölbildung gegen das Blattgewebe durch eine cutinisierte Lamelle
in der Basalwand abgeschlossen (Abb. 6). Es ist also auch hier ganz offensicht-
lich, dass das Mesophyll in Wasser gelöste elaiogene Stoffe in die Drüse abgibt,
die in der Drüse in Öl umgewandelt werden, während das als Transportmittel
dienende Wasser verdunstet oder vielleicht auch in das Mesophyll zurückwan-
dert.

Der Zeitraum, in welchem die Drüsen entstehen und in welchem sie sich mit
Öl füllen, ist bei beiden Familien der gleiche. Ich habe niemals junge Drüsenan-
lagen oder halbfertige Drüsen an vollständig ausgebildeten Blättern gesehen.
Ausnahmslos findet die Anlage der Drüsen in der Knospe, also an ganz jungen
Blättern statt, und die Füllung sämtlicher Drüsenanlagen mit Öl erfolgt während
des Wachstums der Blätter. Am fertig ausgebildeten Blatte ist sie vollendet.
Die Ölbildung hat also offenbar mit der *Funktion* des Blattes, vor allem mit der
Kohlensäure-Assimilation nichts zu tun, sondern sie hängt mit den beim *Wach-
stum* des Blattes sich abspielenden Stoffwechselvorgängen zusammen. Das Öl
kann wegen der die Drüse unten abschliessenden cutinisierten Lamelle nicht mehr
in den Stoffwechsel der Pflanze zurückkehren, es ist also ein *Exkret*. Die Kom-
bination dieser Sätze ergibt die folgende Definition des ätherischen Öls: Die
ätherischen Öle der Compositen und Labiaten sind Exkrete, die Abfallprodukte
der beim Wachstum der Blätter sich abspielenden Stoffwechselvorgänge sind.
Damit wäre für diese Familien dasselbe ausgesagt, was ich früher für die Ruta-
ceen wahrscheinlich gemacht habe, und was auch für die Coniferen zutreffen
dürfte. Bei den Rutaceen findet man in Ausbildung begriffene Drüsen nur in
den kleinsten Blättern in den Knospen, die Vergrösserung der Drüsenräume und
ihre Füllung mit Öl erfolgt nur im wachsenden Blatte, sind die Blätter aber
fertig ausgebildet, so findet eine weitere Vergrösserung der Drüsen oder, was das-
selbe ist, eine Produktion von Öl nicht mehr statt. Auch bei den Coniferen ist
es so; die schizogenen Gänge der Coniferennadeln sind in der Anlage in den

ERKLÄRUNG DER BILDER

1. Junge Drüsenanlage von *Tanacetum vulgare*, Compositae. Mit intacten Zellwänden und Zellkernen.

2. Die Desorganisation der Drüsenzellen beginnt, die Zellwände schwinden, die Zellkerne der oberen Zellen sind schon gelöst, die der unteren in kleine Stücke zerfallen.

3. Drüse gegen Ende der Ölproduction; die Drüse ist nicht gröber als die junge Anlage, die desorganisierten Zellen aber viel kleiner.

4. Junge Drüsenanlage von *Mentha piperita*, Labiatae. Mit intacten Zellwänden und Zellkernen.

5. Die Drüse hat eine grosse, das Köpfchen ringförmig umlaufende Cuticularfalte gebildet, die Zellen haben Zellwände und Zellkerne verloren, die Grösse der Drüse ist noch dieselbe wie vorher.

6. Drüse am Ende der Ölproduction; die Cuticularfalte ist durch das produzierte Öl ausgeglichen, doch ist die Stelle der stärksten Biegung der Falte noch kenntlich, so dass die Ölblase nicht genau kugelige Form hat; die Blase ist erheblich grösser als die junge Drüsenanlage, die Zellen sind aber viel kleiner geworden.

7. Junge Drüsenanlage auf der Epidermis von *Pogostemon patchouli*, Labiatae. Das Köpfchen ist einzellig, die Zelle noch intact.

8. Die Cuticula ist grösser geworden, Zellwand aufgelöst, der Zellkern noch erhalten.

9. Eine junge Drüse in demselben Stadium wie in 8, das einzellige Köpfchen aber mit 2 Zellkernen.

10. Drüse am Ende der Ölproduction; das produzierte Öl hat die Cuticularblase ausgefüllt. die Stelle der Falte ist noch deutlich kenntlich, die Blase hat daher etwa halbkugelige Gestalt, sie ist viel grösser als die junge Anlage, ihre desorganisierte Zelle aber viel kleiner geworden.

Bild 1 bis 10: Vergrösserung 500:1.

11. Anlage einer inneren Drüse im Blatt von *Pogostemon patchouli*; Köpfchen einzellig, aber zweikernig.

12. Ebensolche Drüse gegen Ende der Ölproduction, die Zellen desorganisiert. Vergrösserung 300:1.
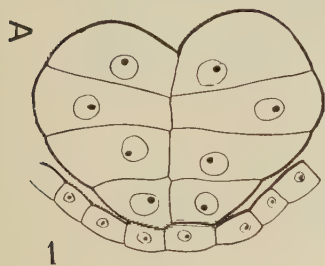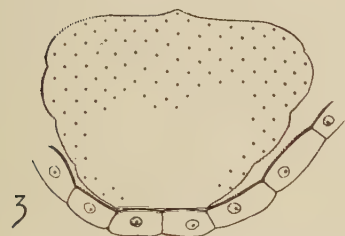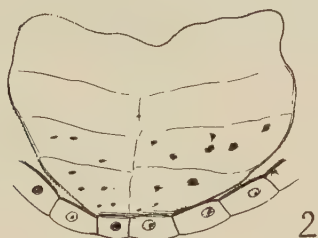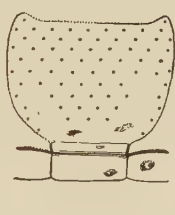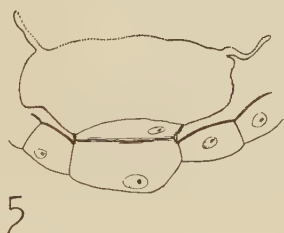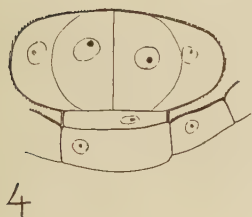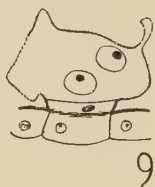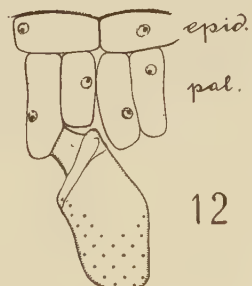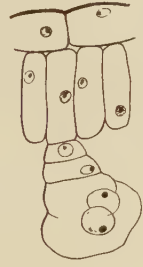
FIGS. 1–12

ganz jungen, noch in der Knospe liegenden Nadeln schon vorhanden, wachsen die Nadeln aus der Knospe hervor, so verlängern sich die Gänge und verbreitern sich, und der Vergrösserung ihres Volumens entsprechend füllen sie sich mit Öl. Dieser Vorgang spielt sich in kurzer Zeit ab, während des nun folgenden, meist mehrere Jahre dauernden Lebens der Nadeln nehmen die Ölgänge nicht an Grösse zu, auch werden neue Gänge nicht angelegt, soweit meine Erfahrung reicht.

Besonders von Chemikern ist zuweilen die Vermutung geäussert worden, das ätherische Öl könnte vielleicht doch gelegentlich in den Kreislauf des Stoffwechsels der Pflanze zurückkehren. Man fand nämlich sehr häufig in älteren Pflanzen einen sehr viel geringeren Prozentgehalt an Öl als in jungen Pflanzen. Nach meinen Beobachtungen ist diese Tatsache sehr einfach zu erklären: die Drüsen fallen nämlich sehr oft von den ausgewachsenen Blättern ab, man findet dann unter dem Mikroskop statt der Drüsen nur die kleinen runden oder rundlichen Epidermiszellen, auf denen die Drüsen befestigt waren, solange das Blatt jung war. Dieses Abfallen der Drüsen wird dadurch ermöglicht, dass die im Niveau der übrigen Epidermis-Aussenwände liegende "Basalwand" der Drüsen, von der ich oben sagte, dass sie cutinisiert wird, in Wahrheit 2 Cutinlamellen erhält, und zwar die eine von der Epidermiszelle, die andere von der darüber liegenden scheibenförmigen "Stielzelle" abgeschieden. Fällt jetzt die Drüse ab, so ist die Epidermiszelle durch die von ihr selbst abgeschiedene Cutinlamelle genügend geschützt, und die Öldrüse bleibt ebenfalls unverletzt.

Noch einige Worte über *Pogostemon patchouli*. Diese Pflanze unterscheidet sich von anderen Labiaten dadurch, dass ihre Drüsenköpfchen statt 8 oder 12 nur 1 Zelle enthalten (Abb. 7). Sehr oft, anscheinend aber nicht immer, enthält diese Zelle aber 2 Kerne (Abb. 9). Der Vorgang der Ölbildung ist im übrigen der gleiche: die Zellwände und die Zellkerne schwinden, die Cuticula wird grösser (Abb. 8) und bildet eine grosse Falte, dann erst beginnt die Ölproduktion und die mit Öl gefüllte Drüse ist deshalb viel grösser als die junge Drüse, etwa halbkugelig (Abb. 10).

Auszerdem hat *Pogostemon* merkwürdige innere Drüsen, die schon Arthur Mayer genauer studiert hat. Die Befunde Mayers wurden bestätigt, ich kann hinzufügen, dass auch die inneren Drüsen oft 2 Kerne haben und dass auch in ihnen die Ölbildung ein lysigener Vorgang ist, insofern sie erst nach Auflösung der Kerne beginnt (Abb. 11 und 12).

THE HISTORY OF THE RHIZOME OF OUR
COMMON PICKEREL WEED[1]

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OLIVER ATKINS FARWELL

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A few years ago when Dr. Klan was visiting the loboratories of Parke, Davis and Company, the junior author brought in some specimens of Pickerel Weed, *Unisema cordata* (Linn) Farwell. The broken rhizome showed a reddish exudation which was so unexpected and interesting that it led to an histological study of the rhizome. The illustrations were drawn by Dr. Klan. The plant is a monocotyledonous aquatic of eastern North America inhabiting the borders of streams and ponds. The stem bears a single cordate leaf and is terminated by a dense spike of blue flowers with a pair of yellow spots; a cluster of root leaves similar to the stem leaf springs from the rhizome. The rhizome investigated was *U. cordata* forma *angustifolia* (Ph.) Farwell.

The rhizome is not a commercial drug nor now used as a therapeutic agent. Medicinal properties have been attributed to it, however, and these are said to be emollient and antiscrofulous. It is said to be similar to the white pond lily for which it may be substituted.

Upon microscopial examination the rhizome shows the typical structure of the monocotyledons having the vascular bundles distributed in all parts of the organ. The endodermis forms a ring which divides the rhizome into the central cylinder and the cortex.

The epidermis of the rhizome consists of isodiametric parenchyma filled with pink anthocyanin. The hypodermal cells are collenchymatous and are arranged in several layers which pass by degrees into a spongy parenchyma consisting of small rounded starch parenchyma and of secretion cells, both forming a network with large intercellular spaces. The vascular bundles are of the collateral type with a sheath of sclerenchyma. In the outer layer of the cortex are numerous groups of sclerenchyma cells. Calcium oxalate forms either very long prisms or raphides which are especially abundant in the inner part of the bark.

The secretion cells (30–100μ) of the cortex are very numerous and have no characteristic localization in the tissue. The spongy parenchyma in longitudinal section shows the pressure of neighboring cells on the secretion cells which as a result of it become flattened in the middle, appearing dumbbell-like. The endodermal cells are much smaller than the surrounding parenchyma and form
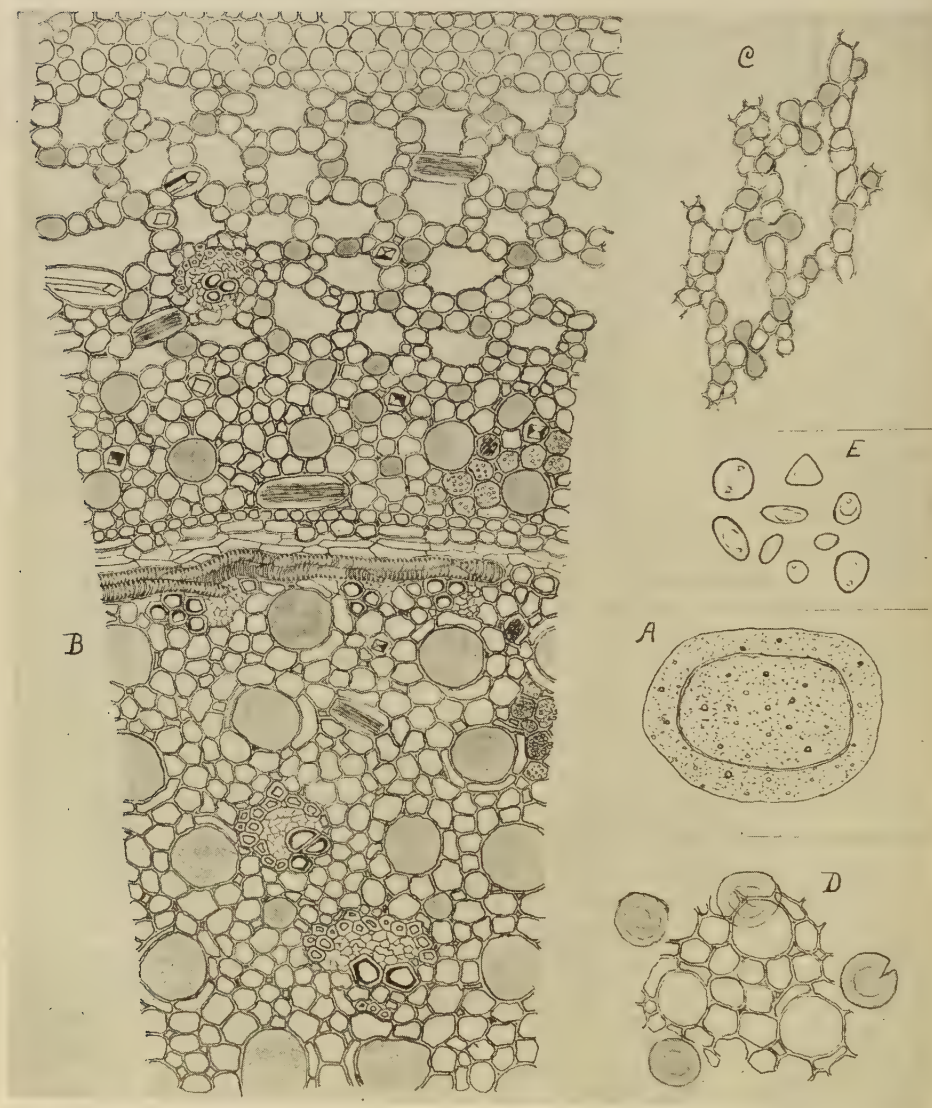
Fig. 1. A transverse section of rhizome. Natural size. B. Transverse section, enlarged. ×120. C. Spongy parenchyma of the cortex, longitudinal section. ×120. D. Secretion cells with resinous contents becoming free. ×120. E. Starch ×400.

a belt running through the entire rhizome. The interior part of the central cylinder forms a layer of vascular bundles which run in all directions so that some of the vessels, in transverse sections, are cut lengthwise showing their spiral thickenings. The connection of the rootlets with the endodermal zone is shown in transverse section by longitudinally cut vascular bundles which run through the cortex in radial direction. This may be seen with the unaided eye. The secretion cells of the central cylinder are much larger (150μ) than those of the cortex; the surrounding epithelium is apparent especially in the older parts of the rhizomes. The collateral fibrovascular bundles do not differ from those of the cortex. The parenchyma tissue of the central cylinder is thickly filled with starch.

The starch. The length of the starch grain averages $3\text{-}6\mu$. The rings are indistinct; in many cases the grains are not visible at all. The grains are of different shape; oval, round, broadly ellipsoidal, and oblong globular, ovoid, rounded. The hilum is hardly visible and is located in the narrower end of the grain.

The secretion cells. The content of the secretion cells is of a resinous character. Thin sections of the rhizome after having been heated at a temperature of about 150° C shows under the microscope a shiny, brown resin which may be crushed by pressing the cover glass and which dissolves very readily in concentrated sulphuric acid into a brown liquid. It is soluble in absolute alcohol and stains red with an alkaline reagent. The unheated tissue treated with concentrated sulphuric acid shows the presence of a volatile oil by staining green the yellow secretion cells.

NEW SPECIES OF WILD EDIBLE FRUITS FROM EASTERN BOLIVIA[1]

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The principal fruit-yielding families of the east Andean region of Bolivia are the Annonaceae, Moraceae, Guttiferae, Passifloraceae, Sapotaceae and Amygdalaceae. The distribution of the 28 species here exhibited among the families, is as follows:

Annonaceae 10, Moraceae 4, Guttiferae 3, Sapotaceae 2, and 1 each in the Passifloraceae, Amygdalaceae, Musaceae, Hippocrateaceae, Caricaceae, Ebenaceae, Verbenaceae, Rubiaceae, and Mimosaceae.

I will refer first to a peculiar and delicious variety of banana of which I have been unable to gain any information, either from botanical or horticultural sources. The fruit is externally of a light pea-green color, when ripe, and very white internally. Its form and general appearance are similar to those of the common yellow banana. It is very sweet and its flavor is peculiarly delicate, suggesting that of the red rather than the yellow variety. I first saw this fruit in the market of Barrancas, on the shore of the lower Orinoco, in 1896 and liked it very much. During the intervening years I sought in vain for information regarding it. In January, 1922, I again saw it in the market of Manaos, Brazil, where I obtained these specimens. It appears to be but little cultivated, though well worthy of being utilized.

The genera of Annonaceae in this collection are *Annona, Rollinia, Trigyneia, Porcelia, Duguetia,* and *Guatteria.* Of the genus *Annona,* I have proposed no new species, although I collected two that I have been unable to determine specifically, and which very probably are undescribed. One species, doubtfully called *A. echinateae* Safford, has been seen by Dr. Safford, who was himself in doubt as to its identity. This species is of interest as being a woody climber. Its fruit differs in form from all others known to me, being regularly cylindrical or ellipsoidal. As it was immature when collected, I am unable to speak of its edible qualities. *A. reticulata,* the well-known custard apple, sugar apple, or bullock's heart, is cultivated at Rurrenabaque and in neighboring localities. *A. dioica* St. Hil. is a peculiar Brazilian species that extends into Bolivia. It grows on open pampas, associating with other shrubbery and is never more than two or three feet in height, so far as I have observed. It has very large tomentose leaves. Its most notable peculiarity is the extremely thick and woody character of its perigone segments. An interesting small-fruited species, the fruit being very regular in its spiral structure, and very glaucous, was purchased in the city market of Manaos,

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[1] Presented before the International Congress of Plant Sciences, Section of Pharmacognosy and Pharmaceutical Botany, Ithaca, New York, Aug. 18, 1926.

but with no clue as to its specific identity or habit of growth. It is a highly prized fruit in that market and sells readily at good prices. *A. muricata*, the soursop, occurs freely throughout the region, both wild and cultivated, mostly on the plains, and is also among the foot hills of the Andes. Its fruit sometimes attains a great size. On my second trip in 1921, I collected this fruit from the identical tree from which I had obtained it 35 years previously. The gem of all the Annonas, *A. Cherimolla*, regarded as one of the most delicious of all fruits, does not occur either wild or cultivated in the lower Andes, so far as I could learn. It is a shrub of cooler regions, and it very possibly cannot be grown at the lower levels. Its place is there taken by *Rollinia deliciosa* Safford, there generally called cherimoya, and so similar to that fruit as to be readily mistaken for it. The trees also, and their habit of growth, are strikingly similar. The fruit is certainly inferior in flavor to the Cherimoya, and it does not keep so well.

If one were to judge by the fruit characters alone, he would be unable to understand why the genus *Rollinia* is maintained distinct from *Annona*. In everything except the floral structure, these genera are identical. In 1886, an Indian brought to me a single ripe fruit, which bore every appearance of being a miniature *Annona*. I found it delicious and having the characteristic flavor of the Annonas. Being unable to secure foliage, or any information regarding the plant, I always supposed it to be a species of *Annona*. In 1921, however, I found this plant growing abundantly in the environs of Rurrenabaque and determined it as an undescribed species of *Rollinia*, which Mr. R. S. Williams had brought me in flower some years previously. With complete material in hand, I am able to describe it under the name of *R. Williamsii*. The plant is a tall slender shrub or small tree and grows thickly among shrubbery where the forest has been cut away.

The most interesting member of the Annonaceae that we have to consider pertains to the little-known and very poorly described genus *Porcelia*. Many years ago, Mr. Williams brought me seeds and fragments of leaves and flowers of a member of this genus. His description of the fruit, which he had eaten, was strongly suggestive of *Guatteria*. So incomplete and misleading were the published descriptions of *Porcelia* that this genus did not occur to me in connection with this plant and I published it, with expressed doubt, as *G. ponderosa*. In 1921, a native brought to me a large branch from a tree bearing the material here exhibited. This was clearly a *Porcelia*, and was evidently of the same genus as the one collected by Williams. This is one of the most remarkable of fruits. Developed from a flower little more than an inch in diameter, it produces three or more circles of separate carpels, three in each circle, which together, when mature, must weigh about fifteen pounds, as judged by the partially grown specimen that I have seen. This fruit is similar to our paw-paw (*Asimina*), but grows on a tree nearly 100 feet high, and with a trunk diameter of two feet or more. It is undoubtedly the largest member of its family. My published description is as complete as the material permits, but leaves some questions unanswered. Flowers taken from the same tree at the same time showed marked differences in size and in the reproductive organs. Since these flowers, together

with buds, were present at the same time as nearly mature fruit, it may be that their variations are due to seasonal conditions. *P. ponderosa*, the species collected by Mr. Williams, is represented by material still more incomplete.

The edible properties of the fruits of *Trigyneia* are little better known than are those of *Porcelia*. In this species also, the carpels are distinct and stipitate, but they are small and usually with only one to three or four seeds. They present the external appearance of follicles or legumes, but are indehiscent and fleshy. The pulp surrounding the seeds is sweet and well flavored. The species here exhibited is a new one, collected by Dr. White, near the Brazilian border and is there eaten under the name "Periquino," a name that I have made specific. Its fruits are larger than any other known species.

Guatteria, of which there are many species in this region, is quite similar to *Trigyneia*, although its carpels have longer stipes and contain but one seed. The flesh is scanty, and the edible properties unimportant.

Duguetia differs in having its numerous carpels densely massed in a globular head, without stipes. They are usually, if not always, more or less coalescent by their pulpy pericarp, so that, from a popular point of view, the fruit represents a many-seeded berry. A number of species that I have eaten possess excellent edible properties, although the pulp is rather scanty. The species exhibited here has much the largest fruit of any known species. It is certainly undescribed, but is represented by only an incomplete mature fruit.

All my fruits of the family Guttiferae pertain to the genus *Rheedia*, although I also obtained a species of *Calophyllum* that is said to yield an edible fruit.

R. Madronya is a well known edible fruit of tropical America, cultivated and marketed under the name Madroña. Its seeds are poisonous and extremely irritant, so that in eating the fruit care has to be taken to avoid biting into the seeds. One of my specimens, collected in an immature state, is doubtfully referred to this species. The others are new. One is named *R. Achachairu*, after the local name, the other *R. Rogaguensis*, because collected near Lake Rogagua.

To me, one of the most interesting of our collections was the fruit of *Hirtella*, of which I collected several species yielding edible fruits, notably those of *H. americana*. My first acquaintance with this fruit was made in 1886, while visiting an Indian family, the members of which had never before seen a white man. The son had been injured and was lying in his hammock. At the time of my visit, his mother was bringing him a gourd full of small cherry-like fruits, of a deep red color, the surface beset with bristles something like those on our wild gooseberry, but less course and rigid. I found these fruits sweet and acid and of an excellent flavor. I could learn nothing of the plant yielding them and often wondered afterward as to their botanical source, until 1921, when I collected them and found that they pertained to this genus. I am not sure that they pertain to my new species, *H. stipitadenia*, here exhibited, but this is quite probable.

It seems strange that a fruit so similar to that of *Hirtella* as to be known by the same local name should pertain to so widely distant a family as the Moraceae, but this is true of the edible drupes yielded by the Pseudolmedias, of which I

obtained two species. It must be admitted, however, that they are in every way inferior to *Hirtella*.

Olmedia, in the same family, yields a drupe that can be regarded as edible only by courtesy. It is very small and of insipid taste, although greedily eaten by many birds. The same may be said of a small-fruited *Ficus* that grows abundantly with it in the river valleys. There is, however, a so-called "wild fig" (Higo del monte) that is not a fig at all, although a member of that family. It is a *Cecropia* that I have named *C. obovata*, and its fruit is said to be very good. I have often seen the fruits of *Cecropia* eaten by birds, and have heard that they are eaten by man, although this is the first species that has ever been definitely pointed out to me as so employed.

In this same family, we have the genus *Pourouma*, noted for its production of a number of edible fruits. The one here shown is a new species, that I have called *P. uvifera*, because its fruit is known locally as Uva del Monte, meaning "wild grape." This name is a very poor one, for although the fruit is of the size and shape of a grape, it differs in containing a single large central seed, like the stone of a cherry. It grows on a handsome, large tree, with digitate leaves like those of our horse chestnut, the fruit hanging in huge clusters about the crown. The pulp is sweet and agreeable, but with little pronounced flavor and very glutinous. Its effect is said to be very constipating, and capable of causing dangerous intestinal obstruction.

Very similar, though much larger, is the fruit of *Sideroxylon bolivianum*, a new species collected on this journey. The fruit of *Lucuma polycarpa*, also of the Sapotaceae, collected before maturity, is said to be much larger and better.

The related family Ebenaceae contributes a number of edible species of Bolivia, though none of the fruits is large or of very good quality. On one occasion, when food was very scarce and hunger was distressing over a long period, I found a small persimmon tree, loaded with fruit, on the bank of the stream and frequently had recourse to it. The pulp of this persimmon was less juicy than that of our east American species, but of similar flavor. It was also much smaller, yet larger than that of the *D. boliviansii* here shown.

A very peculiar drupaceous fruit collected on this trip is *Vitex pseudolea*, which I have so named because its fruit is generally used by the natives as a substitute for the olive. It is very similar in every way, except that it is sweet. When ripe, children are very fond of it, though it has a peculiar flavor that is rarely relished by adults. The tree is a large and very ornamental one, producing its beautiful blue flowers in a dense covering before the appearance of the leaves.

The edible fruits of the Passifloraceae are not so well known as they should be, although some of them are important products in the markets of tropical America. I do not recall any species of *Passiflora* that does not possess an edible fruit, although there are a great number of species about which I know nothing. The pulp of these fruits is usually sweet, and without strong specific flavor. One species that I purcahsed in the city market of La Paz is quite as acid as a lemon and is used for making a lemonade-like drink. I never saw it but once and was unable to learn anything concerning the plant producing it, nor have I been able

to find any botanist or horticulturist who knows of such a species. Many species of *Passiflora*, the fruits of which are eaten, grow in the vicinity of Rurrenabaque. The most common and abundant of them is *P. rivularis*, a species so similar to *P. maliformis* that I find it very difficult to discriminate between them. Its fruits show a great variety in form and size. It is said to have been introduced there from Brazil. The new species here shown is *P. nigradenia*. It produces a very large and highly esteemed fruit.

The fruits of several species of *Tacsonia* are largely marketed in Colombia, and possess unique and delicious flavor. They are commonly known there under the name "Curuba."

Many strange varieties of Papaya were seen in the markets, especially in Manaos, but it was quite impossible to determine whether they were varieties of *Carica Papaya*, or distinct species. The one here exhibited, however, is almost certainly undescribed, and represents a very strange plant. I saw but one specimen of it, growing in the public park of Suri, at a high altitude. It had been brought in from the neighboring forest. Its great peculiarity lay in the fact that its entire crop of fruit ripened at one time or nearly so, and almost completely clothed the trunk and thick branches. The tree is about ten feet in height.

The genus *Inga*, of the Mimosaceae, is a very large one in the region under consideration. Nearly all of the fruits contain an edible sweet pulp in which the seeds are packed in the legumes.

Edible fruits are of rare occurrence in the family Rubiaceae. That of *Genipa americana*, and one or two related species, is largely sold in the market, and must be liked by many people, although to myself and my companions, both its flavor and odor were disgusting. Not so with the fruit of a species of *Alibertia* that I found growing at Rurrenabaque. The fruit of *A. edulis* is cultivated all through tropical America and is very well known. The one here shown is closely related to it, and I was for some time in doubt as to its being a mere variety of that species, but its flowers show it to be quite distinct and I have named it *A. Tutumilla*, the fruit being locally known by this specific name. I found this fruit very agreeable, although some of my companions did not like it.

The remaining fruit of this collection is a species of *Salacia* of the family Hippocrateaceae, collected when the fruit was very immature. I could learn nothing about its quality further than that it is eaten when ripe.

NEUERE UNTERSUCHUNGEN ÜBER SAPONINE UND SAPONINPFLANZEN[1]

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Die Saponinpflanzen haben seit jeher in der Therapie der Völker, als Fischgift und als Hilfsmittel zur Reinigung von Geweben eine grosse Rolle gespielt. Neuerdings haben genauere experimentelle Forschungen über die physiologische Wirksamkeit der Saponine im tierischen Organismus die grosse praktische Bedeutung dieser interessanten Stoffgruppe ins Licht gerückt. So ist es erklärlich, dass von Fachleuten verschiedener Disziplinen die Saponinforschung wieder intensiver betrieben wird. Nach den bisherigen Ergebnissen ist zu erwarten, dass schon die nächste Zukunft manches Geheimnis lüften wird, dass die Saponine seit Jahrzehnten umwebt.

Eine streng wissenschaftliche, die Saponine eindeutig erfassende Definition lässt sich eben wegen der lückenhaften Kenntnis dieser Verbindungen nicht geben. Die übliche Abgrenzung gegenüber anderen Stoffgruppen lautet ungefähr folgendermassen: Die Saponine sind Pflanzenglykoside, welche in wässeriger Lösung stark schäumen, den Blutfarbstoff aus den roten Blutkörperchen herauszulösen imstande sind, auf Fische giftig wirken und durch eine Anzahl von Farbenreaktionen sich charakterisieren lassen. Sie finden sich in zahlreichen Pflanzen vor, in bestimmten Familien so häufig, dass man das Saponinvorkommen als ihnen eigentümlich anführt, z.B. bei den Caryophyllaceen und Sapindaceen. Anderen Familien fehlen sie anscheinend ganz oder sind in ihnen sehr selten enthalten. Ihre physiologische Bedeutung im Pflanzenorganismus ist derzeit vollständig ungeklärt.

Nachstehend sei über Ergebnisse mehrerer Untersuchungen berichtet, besonders solche aus dem Wiener pharmakognostischen Universitätsinstitut, soweit sie auf die Biochemie der Saponine in den Pflanzen Licht zu werfen geeignet sind. Derartige Untersuchungen dürften unter anderem der Systematik von Nutzen sein, die in steigendem Masse die Phytochemie zu ihren Zwecken heranzieht. Die Voraussetzung hiefür bildet die möglichst weitgehende chemische Erforschung der in Betracht kommenden Verbindungen. Wie weit wir bei den Saponinen damit im Rückstande sind, geht schon aus der Tatsache hervor, dass trotz der grossen Zahl von Saponinpflanzen nur aus den wenigsten Saponine rein dargestellt sind. Die Ursache dürfte in der Schwierigkeit der vollständigen Trennung von anderen Pflanzensubstanzen gelegen sein. Nur mit der grössten Mühe lassen sich anorganische und organische Beimengungen von den eigent-

lichen Saponinen vollständig entfernen. Das vielfach benützte Blei- und Magnesiumoxydverfahren haben sich als zu eingreifend erwiesen. Schonender sind die Methoden, bei denen die Saponine mittels Wasser, Methyl-,Aethylalkohol verschiedener Konzentrationen herausgelöst werden, Aether, Chloroform, Petroläther, Benzol zur Reinigung verwendet, im Vakuum gearbeitet, das Prinzip der fraktionierten Lösung, Fällung und Kristallisation und die Dialyse und Elektrodialyse angewendet werden. Ob in irgendeiner Phase der Darstellung eine Aenderung am Saponin stattfindet, lässt die fortlaufende quantitative Ausmessung des Haemolysevermögens erkennen. Die Bedeutung der dauernden Kontrolle der angewendeten Reaktionen und Methoden wird durch die zahlreichen Erfahrungen erhärtet, die man in dieser Hinsicht, besonders in letzter Zeit gewonnen hat. Sehr häufig findet bei der Zerlegung Loslösung von lose gebundenen Zuckermolekülen statt. Noch häufiger wird nicht genügend den Reaktionsmöglichkeiten mit den zahlreichen vorhandenen anderen Verbindungen unter den bei der Darstellung geänderten Bedingungen Rechnung getragen. Bei den Saponinen im Speziellen muss auf das Vorhandensein von Sterinen geachtet werden, da diese die Saponine binden können und die Saponinhämolyse stark beeinflussen. Die Hämolyse wird uns als Kontrollreaktion nur bei den ausgesprochenen, mit deutlichem Hämolysevermögen ausgestatteten Saponinen wertvolle Dienste leisten. Wir müssen aber aus der verschiedenen Intensität der durch die einzelnen Saponine bewirkten Hämolyse, aus dem Umstand, dass schon geringfügige Aenderung des Saponinmoleküls die Hämolyse beeinflusst, und aus den Beziehungen zu den Sterinen schliessen, dass Verbindungen im Pflanzenkörper existieren, welche den eigentlichen Saponinen chemisch nahestehen, als ihreDerivate und Bausteine zu bezeichnen sind, ohne dass sie Hämolyse hervorrufen. Wenn sie uns auch erst in der Zukunft zu beschäftigen haben werden, so dürfen wir doch nicht vergessen, dass sie jede Lesung des Saponinproblems mit einbezogen werden müssen.

Die Analyse der wenigen, als chemische Individuen bekannten Saponine hat ergeben, dass sie glykosidische Verbindungen, eventuell Verbindungen der Glukuron-, auch Galakturon-säure mit Aglykonen sind, die, soweit sie strukturell aufgelöst sind, den Terpenen und Sterinen nahestehen. Für diese Beziehungen sind auch die Farbenreaktionen zu verwerten, die von Saponinen zum Teil in ähnlicherWeise wie von Sterinen gegeben werden. In dieser Hinsicht ist auf eine sehr interessante Erscheinung in der Familie der Primulaceen zu verweisen. Es wurden Samen des gleichen Standortes von *Anagallis arvensis* und *A. coerulea* untersucht. Die Samen von *A. arvensis* wirken stark hämolytisch und geben keine Sterinsublimate, jene von *A. coerulea* enthalten Sterine, zeigen aber nicht den geringsten Grad von Hämolyse. In den Blüten, Stengeln und Wurzeln, sogar in den Fruchtwänden sind in beiden Pflanzen Saponine nachzuweisen.

In der Literatur ist einigemale berichtet worden, dass Saponine und bestimmte andere Stoffgruppen nebeneinander nicht vorkommen, mindestens nicht in denselben Geweben. So sollten sich ätherisches Oel und Saponine ausschliessen. Blausäureglukosiden wurde häufige Koinzidenz mit Saponinen nach-

gesagt. Bei oberflächlicher Betrachtung scheint es zunächst, als wenn Gerb-
stoffe und Saponine sich häufig, wenigstens gewebsweise ausschliessen würden.
Nach dem früher Gesagten muss man sich, sogar wenn wirklich der Nachweis
einer Koinzidenz oder eines Ausschlusses gelänge, vor zu weitgehenden Schlüssen
hüten, da wir nicht wissen, wie weit der heutige Begriff Saponin biochemisch
zusammengehörende Substanzen umfasst, wie viele er ausserhalb seines Kreises
lässt. Aber nicht einmal die behauptete Koinzidenz von Blausäureglykosiden
ist unwidersprochen geblieben. Rosenthaler wendet sich gegen eine solche
Ansicht. Auch für die Pflanzen mit ätherischem Oel müssen wir Einschränkungen
vornehmen. Denn in einigen Umbelliferen, wie besonders *Eryngium*-Arten, in
Sanicula ist Saponin reichlich vorhanden, wie sich in Untersuchungen des
Institutes gezeigt hat.

Was die physiologische Bedeutung der Saponine betrifft, so hat man ihnen
die Rolle von Reservestoffen, von Exkreten und von Schutzstoffen der Pflanze
zugesprochen. Doch ist gegenwärtig viel zu verfrüht, derartige Hypothesen
auszusprechen. Es ist ja in der Tat verlockend, in jenen Fällen, in denen die
Saponine einen grossen Teil der Trockensubstanz des Gewebes bilden, ihnen die
Funktion von Reservestoffen zuzuerkennen, zumal sie Zucker im Molekül führen.
Aber bisher ist bei keiner einzigen Pflanze ein Verbrauch von Saponinen im
Stoffwechsel nachgewiesen worden. Da dem Verbrauch eine hydrolytische
Abspaltung des Zuckers vorausgehen müsste und diese im Organismus auf
enzymatischem Wege erfolgen dürfte, müssten sich saponinspaltende Fermente
in den Pflanzen nachweisen lassen. Doch ist der Nachweis trotz der darauf
gerichteten Bemühungen in keinem Falle gelungen. Ja bisher konnten wir nicht
einmal derartige Fermente in *Aspergillus*, *Penicillium* und *Mucor*-Arten fest-
stellen, die wir auf saponingetränkten Substraten züchteten. Die beiden anderen
Hypothesen können als Verlegenheitsauskunftsmittel bezeichnet werden, die
immer wieder herhalten müssen, wenn man sich über die Bedeutung einer Sub-
stanzgruppe im Unklaren befindet.

Um Anhaltspunkte für die Beurteilung der physiologischen Bedeutung der
Saponine zu gewinnen, muss man vorläufig das Tatsachenmaterial über die
Saponine gewaltig vermehren. Es wurde schon betont, dass vor allem unsere
Kenntnisse in der Richtung der zu den Saponinen zu zählenden Derivate und
deren und der Saponine Konstitution zu erweitern sind. Dann müssen Versuche
über die Entstehung und das Schicksal dieser Substanzen im Pflanzenorganismus
angestellt werden. Für diesen Zweck dürften die mikrochemischen Methoden
besonders wertvolle Dienste leisten. Es hat sich gezeigt, dass für die Lokalisation
der hämolytisch wirkenden Saponine in Gewebsschnitten die Methode der
Hämolyse in den meisten Fällen gute Ergebnisse liefert. Sehr störend erweisen
sich beim Nachweis Gerbstoffe, die bekanntlich die roten Blutkörperchen agglu-
tinieren, in bestimmten Konzentrationen unter Umständen hämolysieren.
Durch Hinzusetzen von gerbstoffbindenden Agenzien zum Blut, z.B. Coffein,
Gelatine konnte die Störung durch die Gerbstoffe, wenigstens wenn Saponine
in nicht zu geringen Mengen anwesend waren, ausgeschaltet werden. Auch auf
andere pflanzliche Haemolytica wie Hämolysine, Cetrarsäure, Agaricinsäure ist

zu achten. In Verbindung mit Farbenreaktionen, mit der Fällung durch Ness-
ler'sches Reagens erhält man derart einen guten Ueberblick über die Verteilung
der Saponine in den Pflanzen. Es liess sich zeigen, dass der häufigste Sitz der
Saponine das Grundgewebsparenchym ist. Auch Epidermen können reichlich
Saponine führen. In den Blättern, die man als Bildungsstätte der Saponine
angenommen hat, sind dieselben nicht immer nachweisbar (*Anemone hepatica*,
Polygala major, *Gypsophila paniculata* u.s.w.). Sind gleichzeitig Gerbstoffe vor-
handen, so kann man nicht selten feststellen, dass die gegen das Zentrum gele-
genen Teile saponinreicher, die peripheren gerbstoffreicher sind. Im Holz selbst
sind Saponine relativ selten. Das Kambium bildet meist eine haarscharfe
Grenze für das Saponinvorkommen, das Stammholz von *Anagallis*, *Digitalis
lanata*, *Polygala vulgaris* ist völlig saponinfrei. Diese Befunde sind noch durch
auf makrochemischen Wege gefundene zu ergänzen. In allen Teilen einer Pflanze
braucht nur ein einziges Saponin vorhanden zu sein, z.B. in der *Primula veris*
die Primulasäure. In anderen Pflanzen finden sich mehrere Saponine. Das
Guairindensaponin ist z.B. hämolytisch sehr wirksam, während das Saponin
des Stammes kaum hämolysiert. In Familien, die durch Gerbstoff-reichtum
gekennzeichnet sind, wie Rosaceen, Rubiaceen, Leguminosen, sind bisher
nur wenige Arten als saponinführend erkannt worden. Umgekehrt sehen wir in
typischen Saponinfamilien wie Caryophylaceen, Primulaceen keinen Gerbstoff.
Es ist interessant, dass die beiden letzt genannten Familien neuerdings in en-
gere stammesgeschichtliche Beziehungen gebracht werden.

Jede Beurteilung der Saponine wird deren physikalische Eigenschaften mit
in Betracht ziehen müssen. Es ist bekannt, dass Saponine die Löslichkeit und
die Verteilung anderer Substanzen in Wasser stark beeinflussen. So erhält
man bei der Extraktion von Pflanzen mit Wasser auch Substanzen, die rein
dargestellt sich in Wasser nicht oder nur schwer lösen. Es ist übrigens bemer-
kenswert, dass die Primulasäure, welche in reinen Kristallen im Wasser schwer
löslich ist, in einer amorphen Form erhalten werden kann, die sich im Wasser
bedeutend leichter löst. In der Pflanze dürfte die Säure in amorpher Form
enthalten sein. Eine weitere wichtige physikalische Eigenschaft der Saponine
ist die Beeinflussung der Passierbarkeit von Membranen durch Lösungen von
Substanzen. Tierkohle in wässeriger Aufschwemmung geht durch Papierfilter
bestimmter Porenweite nicht hindurch, bei Hinzugabe von Saponin geht die
Kohle in das Filtrat. Aber auch lebende Membranen zeigen unter der Saponin-
wirkung eine Aenderung in der Aufnahmsfähigkeit von Substanzen, wie eine An-
zahl von Versuchen in meinem Institute gezeigt haben. So wird die Resorption
von Strophanthin aus dem Brustlymphsak von *Rana esculenta* durch eine geringe
Beigabe von Saponin auf das fünfzigfache gesteigert. Es wurde bei verschiedenen
Säugetieren und Menschen die Resorption von Traubenzucker und Kalzium-
salzen ins Blut nach der Einführung in den Magen ohne und mit Zugabe von
Saponin untersucht. Unter dem Einfluss von Saponin erfolgte ein gewaltiger
Anstieg des Zucker und Kalziumspiegels im Blute. Auch Insulin wird mit
Saponinbeigabe glatt aus dem Magen-Darmkanal aufgenommen, während sonst
Insulin parenteral dem Körper zugeführt werden muss, wenn es in die Blutbahn

gelangen soll. Beim Insulin konnte ausserdem nachgewiesen werden, dass Saponin eine hemmende Wirksamkeit gegen die durch Trypsin und Pepsin erfolgende Herabsetzung der Insulinwirkung besitzt. Diese Saponinwirkung ist umso auffallender, als durch Saponine die Fermentwirkung des Pepsins und Trypsins gegen Kasein in vitro beschleunigt wird. Wo der Angriffspunkt dieser verschiedenen Wirkungen gelegen ist, kann vorläufig nur vermutet werden. Sicher ist jedoch, dass auch in der Pflanzenzelle die Saponine ihre physikalischen und chemischen Reaktionen ausüben müssen und das infolgedessen eine Beeinflussung des Stoffwechsels in der angedeuteten und vielleicht anderen Richtungen, besonders der Ein- und Austritt von Substanzen in die Zellen oder in Zellteile beeinflusst wird. Ob teleologisch gedacht die Pflanze diesen Apparat, wo er besteht, als Einzelbild in der Kette ihrer Mechanismen einstellt, um dort eine nützliche, vielleicht notwendige Funktion auszuüben, ist eine andere Frage. Bei einigen Saponinen könnte auch die hydrolytische Spaltung, wenn sie regelmässig und leicht erfolgt, in den Dienst der Turgorregelung gestellt werden, wie man es sich für die chemisch den Saponinen sicher sehr nahestehenden glukosidischen Herzgifte der Digitalis vorstellen kann.

Versuchen wir unsere Ausführungen zusammenzufassen, so kann gesagt werden: Die gegenwärtig übliche Abgrenzung der Saponine gegenüber anderen Pflanzenstoffen berücksichtigt nur jene Substanzen, die als "typische" Saponine durch verschiedene Farbenreaktionen, ihr physikalisches Verhalten, besonders der Hämolyse gekennzeichnet sind, umfasst aber nicht Derivate von biochemischen Verwandten, bei denen die Hämolyse, eventuell andere "Saponinreaktionen" versagen. Jeder Versuch einer Klärung des Saponinproblems muss diese Derivate in die Beurteilung mit einbeziehen. Sicher bestehen engere Beziehungen zu den Phytosterinen. Man könnte die Vorstellung haben, dass die Saponine zu den Sterinen etwa ähnliche Beziehungen wie die typischen Alkaloide zu den Proteiden aufweisen. Die interessanten, praktisch so wichtigen physikalischen Eigenschaften der Saponine, der Löslichkeitsbeeinflussung und der Beeinflussung des Hindurchtritts von Substanzen durch tote und lebende Membranen, müssen auch in der Pflanzenzelle den Stoffwechsel in verschiedenen Richtungen beeinflussen.

LICHENS OCCURRING UPON OFFICIAL DRUGS[1]

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Since lichens are found only where there is at least some sunlight, their number decreasing with the diminishing intensity of light, disappearing completely in the deep shade of a dense forest or tropical jungle, they are necessarily restricted to the aerial portions of our drug plants, and to those parts where the light conditions are satisfactory. They can be found on the bark of the twigs, of the branches, of the trunks, and even on the leaves. I have often wondered why I have not found them on such leaves as *Eucalyptus*, or upon the scale-covered twigs of *Thuja*. *Thuja* growing in the tropics is thickly covered with epiphyllous lichens, but when growing in its natural habitat seems to be devoid of them.

It is naturally upon the "barks," that we expect to find and do find lichens. An examination of the official barks shows that of the 27 listed, only 12 can possibly have lichens growing upon them, the other 15 being either *inner* barks, such as *Ulmus*, *Pinus alba*, etc., or *root* barks, such as *Sassafras*, *Viburnum prunifolium*, etc., or, if stem barks, have been rossed, as *Prunus virginiana* and Canella. Thus of the U.S.P. drugs, only Cascara Sagrada, Cinchona, Granatum, and possibly Cinnamomum, can have lichens growing upon them; and of the N.F. drugs, Xanthoxylum, Frangula, Mezereum, Condurango, Coccillana, Viburnum Opulus, Tonga, and Cascara Amarga, can have them. Some of these barks are literally covered with lichens, giving, I am quite sure, an indication where the plant from which they were taken grew. As to Granatum, their presence shows at once that the bark in question is stem bark and not root bark.

I have been studying the lichens found upon official barks for a number of years, nevertheless, this paper can still be considered a preliminary or introductory one. A study of this kind, from its very nature, is never complete— a new lot of bark, and perhaps another lichen is added to the list. Then again, many of the species of lichens that are found may be so fragmentary that their determination may be for the time impossible, and one refrains from writing about them hoping sooner or later to be able to decide upon them. So in this paper I shall present no extended lists of the lichens that I have found thus far on any of the barks. These must be withheld for further study. Instead, I shall present to you some of the possibilities of a study of this.kind, and hope to impress upon you that a study of these plants, generally considered insignificant, may really be worth while.

The literature upon the subject is rather meager. Feé in 1824, wrote his "Essai sur les Cryptogames des Ecorces Exotiques Officinales." Since this time

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[1] Presented before the International Congress of Plant Sciences Section of Pharmacognosy and Pharmaceutical Botany, Ithaca, New York, Aug. 18, 1926.

apparently nothing more has been published on the subject, except a paper by Senft. Tschirch, in his "Handbuch der Pharmacognosie," Band I, Teil 2, page 384, states what Senft has contributed to the subject. Feé's paper is the important one. One notes with surprise that he describes 298 species, and 17 varieties; these occur upon but five of the barks, official at that time,—Cascarilla, Cinnamomum, true Angustura, false Angustura, and Cinchona. Cascarilla and Angustura, both the true and the false, are now no longer official, and the species of Cinnamomum and Cinchona that he studied probably no longer furnish official Cinnamomum and Cinchona. At no place does he make lists of the lichens found on each of the five drugs, nor does he mention which of the species found are most common. Among his statements about lichen-covered barks, is the following: "Cette grande quantité de lichens doit necéssairement influer sur la qualité des medicament qu'il faudrait débarrasser de ces parasites." Tschirch, however, writing on this subject, states that he does not think that lichens have any effect upon the quality of the preparations made from barks with them. One of my problems is to find out whether there is any difference between a preparation made from a bark covered with lichens, and one made from the same bark without lichens. Theoretically, there should be a difference.

My studies of lichens indicate that frequently a species of plant has its own particular lichen flora; thus, a white pine forest has its own peculiar lichen flora, which is quite different from the lichen flora found in the spruce forest, and neither of these floras is like the one peculiar to an oak forest. Should this be true for our drug plants, and I see no reason why it should not be true, it would mean that Cascara Sagrada, for example, has its own peculiar lichen flora, that Cinchona has its own, and so on for each of our bark drugs. Of these lichens, peculiar to the drug, one would be the dominant species. There also may be one or two or even several other species constantly associated with this dominant species. So true could this be, that given any lot of a drug, one would be sure of finding growing upon it the lichens peculiar to the drug. My studies seem to indicate that this is more or less true. Thus upon Cascara Sagrada, I always find *Thelotrema lepadinum* Ach. It is a species of lichen that I have found only upon Cascara Sagrada; so constantly true is this, that I believe I can say that given an official bark, and it has *Thelotrema lepadinum* growing upon it, it is Cascara Sagrada.

Two problems present themselves in this connection: (1) whether the drug will have the same lichen flora, irrespective of its habitat, and (2) whether the drug will have the same lichen flora irrespective of the place upon the plant (that is its height from the ground) from which it was taken. As to problem (1), most of our drug plants have restricted habitats, thus, Cascara Sagrada is restricted to the north-western part of the United States and British Columbia, and the lichen flora may be much the same throughout this area; but should the regions from which a drug comes be markedly different, there is quite a difference in the lichen floras of the different regions, and it becomes quite possible to tell the region from which the drug came from the lichens. As to problem (2), my

studies indicate that there is a marked difference in the lichen flora of the region near the ground and higher up on the tree. Lichens are distributed in zones; those near the base of the tree are different, upon the whole, from those higher up, and these again are different from those near the summit of the tree. Whether this knowledge is of any practical value can only be ascertained by further study and experiment. It may be quite possible to tell from its lichen flora whether the bark was collected from the base of the plant or from its very top; likewise, it may be quite possible that bark collected from one part of the plant may be far more valuable, that is, richer in medicinal virtues, than when collected from another part.

As to the forms of lichens which are generally found upon the barks, as they appear in market, we note that, as might be expected, crustose forms predominate, next in order come foliose forms, and only rarely do we find fruticose forms, these as well as the larger foliose forms being readily removed with the mosses that may also be growing upon the bark.

Since lichens are so constantly present upon some of our drugs, it would seem that a little more attention should be given to them than is given at present. Perhaps it may be going too far to say that the Pharmacopoeia and the National Formulary, should state which lichens are likely to be found upon the several barks, but every dispensatory, and every book on pharmacognosy should not only state which species of lichens have been found upon them, but should give enough information to enable the student to identify the species he finds. The study of lichens is no more difficult than many of the other studies that we have to master. I recommend it as one of the very fascinating ones.

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DIGITALIS, THE HEART TONIC[1]

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The aim of the discussion was to give a rather complete survey of the information available to-day on this plant (commonly called foxglove or fairy-fingers) and its products.

Its present distribution on the American Continent is in the states of Oregon, Washington, and Maine; likewise in Columbia; on the European Continent it occurs in Ireland, Wales, Germany, etc. The introduction of *D. purpurea* in medicine by the Englishman Dr. Withering (1753) leading to the world recognition of this today indispensable drug was referred to and mention made in some detail of the extensive chemical and physiological work done up to date mainly on the leaves of this one species, and the more limited study of other *Digitalis* species. Microphotographs were shown exhibiting characteristics of the glucosides and the hydrolytic products thus far isolated (see Table 1).

TABLE 1. DIGITALIS COMPOUNDS

Glucoside		Hydrolytic Products	
		Genins	Sugars
Digitoxin ($C_{44}H_{7i}O_{14}$) M.P. 252°C	$\longrightarrow$	Digitoxigenin ($C_{2i}H_{36}O_4$) M.P. 245°C	+2 Digitoxose ($C_6H_{12}O_4$) M.P. 110°C
Bigitalin ($C_{40}H_{64}O_{14}$) M.P. 282°C	$\longrightarrow$	Bigitaligenin ($C_{22}H_{3i}O_5$) M.P. 232°C	+3 Digitoxose ($C_6H_{12}O_4$) M.P. 110°C
Gitalin ($C_{17}H_{28}O_6$) M.P. 245°C	$\longrightarrow$	Gitaligenin ($C_{11}H_{18}O_3$) M.P. 222°C	+ 1 Digitoxose ($C_6H_{12}O_4$) M.P. 110°C
Digitonin ($C_{50}H_{82}O_{25}$) M.P. 225°C	$\longrightarrow$	Digitogenin ($C_{26}H_{42}O_6$) M.P. 250°C	+2 Glucose ($C_6H_{12}O_6$) 2 Galactose
M.P. = Melting Point			

The author then discussed in detail the photographs and microphotographs on hand, and the progress made in his laboratory dealing with the morphology, microchemistry, and chemistry of the seed of *Digitalis purpurea*, reputed to be ten times stronger in cardiac action than alcoholic extracts of the leaves. Especially significant was his detection of digitoxin in the seeds and the isolation of over 30 per cent of a drying oil.

He mentioned his results in collecting seeds and leaves of definite strains, his progress in regeneration of the leaves, the importance of fresh collection and

quick drying of the leaves, and the difficulty in milling the seed on account of its small size and hard seed coat. He demonstrated his newly constructed apparatus found useful in the separation and purification of the active chemical constituents.

He finally outlined the future of the work particularly as directed to the study of the plant in its chemical life cycle, and to include in the scope, ultimately if possible, the whole group of species.[2]

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[2] The following participated in the discussion: Professor Fisher, Minnesota College of Pharmacy, who is now growing both *D. purpurea* and *lutea*; and Professors Canis, Gathercoal, Rusby, and Youngken. Professor Youngken had studied *D. siberica*. Professor Youngken, supported by Professors Canis and Rusby, urged the greater utilization of seedlings in general studies of standardization, recalling the effect of active substances on extent of growth. All who took part in the discussion agreed with the leader as to the present inadequacy of physiological and chemical standardization and the need for complete pharmacognostical (botanical and chemical) records as a basis for therapeutic study.

THE GROWTH AND COLLECTION OF
CASCARA SAGRADA[1]

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For the last four years the cascara tree has been under the observation of interested members of the faculty and senior students at the Oregon State College and it is the purpose of this paper to summarize briefly the general methods employed in the industry and the results we have obtained.

Cascara (*Rhamnus Purshiana* De Candolle) was discovered on the banks of a tributary of the Columbia about 1805 by members of the exploring party of Lewis and Clarke. It was first noted on the California coast in 1816 by a Russian naturalist, Eschscholts. It has been grown under cultivation at the Arnold Arboretum sine 1873.

The tree is claimed to have been known since the early part of the nineteenth century to the Mexican and Spanish priests of old California. It was known by the Spanish name cascara sagrada (sacred bark), so named because the wood was supposed to be identical with the "shittim" or "chittim" wood used in the Ark of the Covenant. The same wood was also said to have been used for dowel pins in the construction of King Solomon's Temple.

The diameter of the average cascara tree is about 6 inches, twelve inches being rare. In height the tree seldom exceeds 60 feet, with approximately half this altitude the rule. The normal yield per tree is about 25 pounds of green bark.

On account of the scattered and remote growth of the species, the industry is followed by few persons and only the expert and experienced collector is able to wrest a livelihood from the business which, on account of weather conditions, is only profitable in late spring and early summer.

Properties. The American Indians were the first to teach the properties of the bark. The gathering of the bark differs in no essential aspects from the methods of the original homesteaders sixty years ago. The tree looks much like common white alder and frequents most lowlands, cut over timber lands, and stream margins, persisting commonly with species of fir, hemlock, and spruce.

Prof. Justin Powers, of the School of Pharmacy, Oregon State College says, "Although species closely related to it have been used as cathartics from a very early date, it is only within comparatively recent times that cascara sagrada has come into general use. Among the related species which it has largely replaced are *Rhamnus cathartica* and *R. frangula*.

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[1] Presented before the International Congress of Plant Sciences, Section of Pharmacognosy and Pharmaceutical Botany, Ithaca, New York, Aug. 19, 1926.

Without doubt cascara sagrada was first used by the American Indians, from whom its virtues were learned by the Spanish priests of old California. Since being introduced to the medical profession in 1877, there is probably no single drug which so quickly attained popularity. That this popularity was deserved is shown by the fact that it is still held in high esteem and has in a large measure replaced several similar drugs of our materia medica.

The first publication concerning the medicinal value of cascara sagrada was that of Dr. J. H. Bundy of Calusa, California, in 1877. To Parke, Davis and Co. of Detroit belongs the credit of first offering a legitimate preparation of the drug to the medical profession, immediately following Dr. Bundy's publication.

The extended use of cascara sagrada during a period of nearly fifty years and numerous special investigations have not yet afforded a definite determination of the chemistry of the active constituents. In this field lies an unusual opportunity for research.

For the treatment of habitual constipation due to the lack of functional activity of the intestine or lack of digestive secretions, cascara sagrada has no peer. It is said to be more active and more certain in its actions than any one of the closely allied species which are used similarly. In the use of most laxatives, gradually increasing doses are necessary to produce their effects, but this is not true of cascara sagrada. It not only increases the secretions of the gastro-intestinal canal, but, due to the bitter principle, it acts as a tonic, improves the appetite and digestion, and prevents the constipation which usually follows the use of similar drugs. In fact, so marked are these characteristics that the dose may be gradually diminished and finally discontinued without the return of constipation.

Plantings. In 1914 experimental work on the planting of cascara was started at the Canadian Experimental Station of the Dominion Department of Agriculture at Sidney, on Vancouver Island. Unfortunately, the area which the trees occupied was needed for other purposes, and the planting was later destroyed, before satisfactory data on the growth under cultivation could be obtained.

Several small plantings in the Willamette Valley have been started principally by nurserymen. It should prove interesting to watch the development of these young seedlings under cultivation. Up to the present they have been growing very well, and in 12 to 15 years the trees should be large enough for peeling.

The Forest School has successfully transplanted wild stock and has also produced plants from seed and from layers Fig. 1, B. Thus far cuttings have been a failure. About $\frac{1}{4}$ acre of seedlings are now growing nicely in the Forest Arboretum near Corvallis.

Peeling Operation. A tree is "spotted" and if small is peeled standing, otherwise it is peeled as high as the operator can reach and then felled for the easy removal of the remainder. A lateral incision is made in the bark with a sharp knife, then by means of a thin metal spud, usually made from an auto spring leaf, the bark is cleft from the trunks and limbs. The strips are then placed in

Fig. 1. A. Animal damage to sprouts. B. New cascara plant from layering.
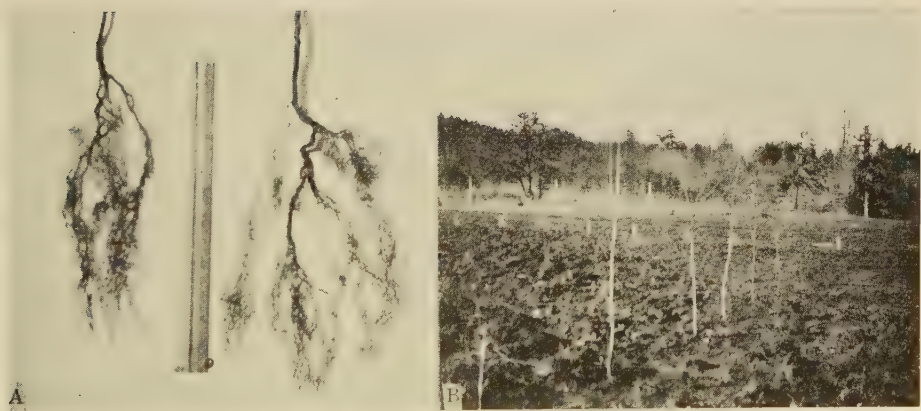
Fig. 2. A Root system after one year in transplant bed. B. View of cascara plantation, Oregon State College.

gunny sacks and carried on the peeler's back to a horse trail, where the sacks are placed upon animal's backs and conveyed to drying grounds.

Drying consists of exposing the raw bark to the sun's rays on wooden platforms or canvas spread upon the ground, which prevents mold. During the rainy months the bark is peeled under shelter. The bark is then reduced to chips, usually by hand, although recently several motor-driven breakers have been installed in the region. After reducing the chips they are sacked and ready for sale.

Good peelers under favorable conditions can peel from 100 to 250 pounds of dry bark per day, and with a price of from 10 to 12 cents per pound, have been known to make twenty to thirty dollars per day.

Merchandizing. The first buyers are usually local warehousemen who in turn sell to pharmaceutical house agents, the material moving to water or rail transportation. The commercial Cascara is then ready for shipment to the world markets. London, England, is the single largest purchaser of Cascara, about 1200 tons yearly finding its way to this market, and thence to other European cities. From 5,000,000 to 7,000,000 pounds on the average are cut annually in the coast ranges of Western Oregon, Washington, and California. A much smaller amount is produced in British Columbia, the only other place where this tree grows in commercial quantities.

Future. Dealers and forestry officials who have studied the methods practiced by the industry prophesy the end of the crop within a few years if the present conditions continue. According to government estimates in 1922, over 500,000 trees were peeled.

Each year it is necessary to gather from the more remote and inaccessible areas to meet the increasing demands. Areas are already being peeled over for the second and third time. This second and third peel is said to come from trees that were too small to yield heavy enough bark at previous cuttings. The trees peeled today are much smaller in the aggregate than trees peeled twenty or thirty years ago.

One means of lengthening the life of the industry would be to find a satisfactory method for using more of the tree. In view of the fact that the thinner bark yields the highest per cent of the desired chemicals, it may be possible and profitable in the future to grind up the smaller twigs and limbs for extraction of the contents. This process would permit of much closer utilization, and should make the growing of the tree on a commercial basis more profitable.

ACTIVITY OF EXTRACTS FROM THE BARK, TWIGS, AND WOOD OF RHAMNUS PURSHIANA[1]

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The continued increasing demand for the cathartic extractive of cascara sagrada bark, accompanied by a correspondingly increasing difficulty in the collection of present and future supplies of bark, due to the receding of the line of easily accessible bark from the railroads and highways, has caused a group of workers interested in this drug to study the possibility of utilizing the twigs and wood of *Rhamnus Purshiana*. With no definite plan of reforestation, other than the specification in "stumpage" permits which specifies that the tree must not be cut closer than 4 to 6 inches from the ground, thus giving the stump a chance to sprout, it is evident that the supplies are more difficult to obtain as the years go on. As I mentioned above, the collection area each year is moved back farther and farther from the transportation lines, thereby increasing the labor necessary to bring the bark to market, adding at the same time a higher cost to the drug. In the meantime, while collection of the bark presented no serious difficulty, no thought was given to the possibility of using the wood or twigs, the latter having been a total loss. Within the last few years more and more interest has been aroused in this direction, and at the present time, considerable research work has been started along these lines.

In this connection I have been asked to give to this section of the Congress a review of the work carried on by R. H. Clark and K. B. Gillie of the University of British Columbia, and published by them in the American Journal of Pharmacy, June, 1924, and also a review of my paper on activity of cascara twigs and bark presented at the Plant Science Seminar at Minneapolis in August, 1925.

The objects of the Clark and Gillie investigation were:

(1) To determine the possibility of utilizing the wood of the cascara tree in making an extract with sufficient activity to make it a commercial source of this laxative.

(2) To study the extent of the griping action of extracts from fresh bark, and the possibility of eliminating this griping action by chemically curing the extracts with a view toward abolishing the requirement of ageing the bark from one to three years as now required by the pharmacopoeia.

(3) To note the differences in activity of extracts prepared from bark varying in age and of varying habitats.

(4) To determine whether or not the active principle is a glucoside.

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(5) To find a physical or chemical standard by which the active constituent of the extract might be judged with some degree of accuracy.

The extracts were made from fresh bark and wood according to the directions of the United States Pharmacopaea IX, using Type D process. An attempt was made to cure the extracts chemically in order to overcome the present practice of holding the bark for at least one year before using and so destroying the griping action which is ascribed to preparations made from cascara bark which has not been aged. In the collection of bark, only two trees were found which for a certainty yielded a griping preparation. Since it was believed that the action taking place in ageing was oxidation, one pound of 3 per cent hydrogen peroxide was added to 500 cc. of the extract and evaporated to the original volume.

With a view toward establishing physical and chemical properties of the extract which would have a direct relationship to the physiological activity, determinations for specific gravity, total solids, ash, manganese number, and percentage of reducing sugars before and after hydrolysis were made.

Relative to the nature of the active ingredient of cascara extracts, the point is made that if it were a glucoside, complete hydrolysis of the active ingredient should destroy its activity. In testing this out, two samples of bark were extracted, percolated, and the percolate divided into two parts. One half was hydrolyzed by boiling with a known quantity of hydrochloric acid and then neutralized with sodium bicarbonate; the other half was retained as a check in comparing the laxative effects of the hydrolyzed and unhydrolyzed extracts.

The physiological tests were made at the Vancouver General Hospial. One cubic centimeter was administered to patients only when they required a laxative. Account was kept of doses given and of results obtained. The efficiency was calculated by dividing the number of times the dose was effectual by the number of doses given.

The conclusions of Clark and Gillie's experiments are:

(1) The physiological tests of the extract from the wood gave an average efficiency of 38 per cent while that of the bark was 53 per cent, making the wood extracts 71 per cent as efficient as the bark extracts. The percentage efficiency of wood extracts varied from 0 to 78 per cent and it is believed that if the wood extracts were made two or three times as concentrated as the bark extracts, they would prove to be equally as effective.

(2) Regarding the griping action of the extracts from freshly cut bark or wood, it was not at all common; such marked action was observed in only two cases. The trees yielding this bark grew within city limits and had a very rapid growth. The bark was darker than usual. Oxidation of this griping extract with hydrogen peroxide produced the desired result but due to lack of such extracts, the experiment could not be duplicated.

(3) Habitat and seasonal rainfall appear to have a marked effect on the activity; bark and wood collected at the end of an abnormally hot and dry summer yielded a 44 and 29 per cent efficient extract while the average for all other extracts was 61 per cent for the bark and 48 per cent for the wood. Collection late in the season seems to have no marked effect on the efficiency.

(4) In the case of wood extracts, the age of the wood appears to have little influence on the activity, but with the bark there is a decrease of activity with age.

(5) Complete hydrolysis did not destroy the activity of the extract, consequently the active principle does not appear to be a glucoside, though it might be a hydrolytic product of one.

(6) The physical or chemical properties bear no close relationship to the activity of the extracts. There is a wide fluctuation of values for each of the determined properties.

The Lilly Research Laboratories have manifested some interest along this line although the work has not been as extensive as that of Clark and Gillie. The work carried on in Indianapolis had to do with the extractive of twigs, young bark, old bark, and medium-aged bark. The bark and twigs were collected during early summer of 1924 and aged for one-half year, after which period a portion of it was used in making a fluid extract according to U.S.P. IX directions (p. 179) by Type D. Process (p. 176).

A chemical analysis was made for anthraquinone content of these preparations according to the gravimetric method recommended by H. C. Fuller (Journ. Assoc. of Official Agric. Chemists 7: (p. 7).

The method in brief consists of introducing 5 grams of the drug into a 500 cc. Erlenmeyer flask, adding 200 cc. of chloroform and 50 cc. of 25 per cent sulphuric acid. This is attached to a water cooled reflux condenser, using a cork stopper covered with tin foil, and boiled for 2 1/2 hours. After cooling, the contents of the flask are transferred to a separatory funnel, as are also the washings with a little fresh chloroform. The chloroform solution is drawn off and 50 cc. of chloroform added to the acid mixture, agitated, and run into chloroform previously collected after separation has taken place. The procedure is repeated, the acid mixtures being discarded.

About 2/3 of the solvent in the chloroform shake-outs is recovered by distillation, the balance being poured into a separatory funnel and thoroughly washed to remove final traces of anthraquinones. This is agitated with 25 cc. of 10 per cent sodium hydroxide solution, the chloroform drawn off and given a second treatment with 10 per cent hydroxide solution. Draw off the chloroform and wash with 25 cc. of water.

The alkaline solutions and washings are united, excess hydrochloric acid added and shaken out three times with chloroform. The acid is discarded, and the chloroform solution washed by shaking with 50 cc. of water. After completely settling, the chloroform is filtered through cotton, and a portion of the solvent recovered by distillation. The balance is poured into a tared dish, and evaporated. This is dried at not over 100° for 30 minutes, cooled in desiccator and weighed. The weight represents the total anthraquinone bodies in the drug.

The results obtained are as follows:

F. E. of twigs;   0.322 gms. of anthraquinone bodies per 100 cc. of F. E.
F. E. of young bark;   0.918 "   "   "   "   "   "   "   "   "   "
F. E. of medium bark;   0.970 "   "   "   "   "   "   "   "   "   "
F. E. of old bark;   1.40   "   "   "   "   "   "   "   "   "   "

The percentage content of anthraquinone bodies in the fluids is:

Twigs..............0.322   Medium bark..........0.97
Young bark.........0.918   Old bark.............1.40

The total of anthraquinone bodies in fluid extracts prepared from the regular run of the drug varied from 1.40 to 2.08 per cent.

The extracts prepared were also tested physiologically. The experiment consisted of starving a group of dogs for 24 hours before administering any of the drug. At the end of that time, they were given 1 cc. doses of these fluid extracts in capsules and placed on regular diets. These doses were given at weekly intervals. The comparison as observed, is as follows:

Old bark	90 to 100 per cent
Medium bark	75 per cent
Young bark	75 to 80 per cent
Twigs	40 to 50 per cent

These results seem to fall right in line with what might be predicted from the chemical analysis—the greatest physiological efficiency from the drug containing the highest percentage of anthraquinone bodies. The preliminary work carried on so far would hardly justify the use of twigs as a possible source for the cascara cathartic extractive, unless perhaps the concentration might be made about twice that of the U.S.P. bark, so that 1 cc. of the fluid extract would be the equivalent of two grams of the crude twigs.

With the activity of two grams of twigs in 1 cc. of the extract, the percentage of solids present would not exceed that of the extracts prepared from the bark. In making a determination for solids in the four extracts, the following results were obtained:

Old bark extractive	26.24 gms. per 100 cc.
Medium bark extractive	29.01 " " " "
Young bark extractive	28.43 " " " "
Twigs extractive	12.88 " " " "

From this it would seem that the twigs could be used as a source of the active cascara extract as well as the wood, and that the activity is found throughout the tree, although to a greater extent in the bark than in the wood or twigs.

SOME NOTES ON THE CONSTITUENTS OF CASCARA SAGRADA AND OTHER CATHARTIC DRUGS[1]

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Our work in this field for the past two years has dealt with the refinement of the quantitative methods for the assay of these drugs and their preparations, and with a further investigation into the manner of combination of the hydroxy-methylanthraquinones in the unmanufactured drugs. The weight of evidence points indubitably to the presence of the greater part of these derivatives of the anthraquinone nucleus in the form of glucosides or related compounds.

In the quantitative assay of these drugs and their preparations, extraction with such solvents as chloroform during the progress of a hydrolytic treatment with dilute sulphuric acid gives a threefold yield of emodin and related substances as compared with the yield obtained by extraction in the absence of any hydrolyzing agent. This is recognized by Daels and all of those chemists who have attempted a modification of his assay process, in their acceptance of the terms "free" and "combined" anthraquinones.

Thorpe and Miller have obtained from *Rhamnus frangula* the substance frangulin, a definite compound having the character of a glucoside, and have demonstrated that emodin and rhamnose are the products of hydrolysis. Beal and Gunton likewise have obtained this same substance and have also succeeded in the synthesis of a similar substance from emodin and rhamnose obtained from different sources. Furthermore, this synthetic substance, mixed with natural frangulin failed to produce any depression of the melting points of the two substances which themselves were identical.

Dohme and Engelhard have asserted that cascara sagrada does not contain emodin, but only a glucoside which yields emodin on hydrolysis. The writer has yet to find a specimen of this bark which does not yield free emodin to such solvents as chloroform and ether, but has no assurance that this was not formed from the splitting of glucosides of emodin during the curing operations. They named this substance purshianin and demonstrated that it possessed in concentrated form the aperient properties of the natural drug.

Jowett criticized rather severely the finding of Dohme and Engelhard, claiming that they had not furnished conclusive proof of the identity of this substance and that his investigations had failed to show that any trace of this substance was present. Pietsch and again Tschirch and Monikowski have obtained a glucoside-like material from this drug which they have called peristaltin. Lately Dohme and Engelhard have verified their findings and proposed

a method by which they claim it to be possible to determine the actual glucosidal content by precipitation with lead subacetate, after a preliminary clarification with lead acetate.

Very recently, with the aid of Mr. H. L. Tschentke, the writer has undertaken a method for the isolation of the possible glucoside-bearing fraction of cascara bark. Having observed that the glucosidal material is apparently insoluble in ether, both the drug and the concentrated alcoholic extract of the drug were exhausted with ether to remove all trace of free anthraquinones. The material was then percolated with ethyl acetate to complete exhaustion, this solvent distilled, and the concentrated extract mixed with a large volume of ether. A precipitate was obtained which was washed with ether until free from all ether-soluble material, and then dissolved in alcohol and hydrolyzed with the aid of hydrochloric acid. The hydrolyzed product responded to the Borntraeger reaction for hydroxyanthraquinones and to the Molisch test for carbohydrates.

The precipitate described in the preceding paragraph is quite flocculent and was only to be obtained from a dilute extract. When a much larger quantity of drug was extracted it became necessary to evaporate the ethyl acetate extract to dryness and merely wash it with ether as long as the washings gave a positive Borntraeger reaction. By hydrolysis of this larger quantity of material, it became possible to obtain crystals which were identified as emodin and an aqueous solution from which glucosazone was obtained by condensation with phenyl hydrazine. Steps are now under way to determine to what extent this material represents the active principle of cascara sagrada.

In the assay of cascara it has been the practice to follow the gravimetric extraction method outlined by Daels, in which a distinction is made between "free" and "combined" anthraquinones. The first group includes those which are extracted directly by chloroform, or ether, from the drug or its preparation, while the second comprises only those which may be extracted by these solvents after hydrolysis with acid.

In particular, three substances are found to contaminate the extracted anthraquinones. The free anthraquinone is contaminated with fatty material, partly in the form of free fatty acids, partly as rhamnol arachidate and similar esters. The same type of contaminating substances are found, though in lesser amounts, in the combined anthraquinones. These acidic impurities naturally accompany the hydroxyanthraquinones through all purification operations where the solubilities in acid and alkaline solutions govern the extractions.

Mr. Tumminkatti has found that the hydroxyanthraquinones are all quantitatively adsorbed by decolorizing carbons from their solutions in the immiscible organic solvents, while the fatty impurities are retained in the solution. It has thus become possible to determine the extent of this type of contamination of the anthraquinone residues and to determine the pure anthraquinone by difference.

It has also been determined that the combined anthraquinones are contaminated by two other substances; one soluble in both water and chloroform and yellow in color, the other insoluble in water, slightly soluble in chloroform,

and moderately soluble in alkali and brown in color. These contaminating substances in many instances amount to more than one per cent of the drug, in fact, in some cases they are equal to or greater in amount than the anthraquinones. However, it has been found that the anthraquinones may be freed from these substances by very simple operations, namely, solution in alkali, precipitation with hydrochloric acid, filtration and resolution of the anthraquinones by washing the filter with alkali.

A last point worthy of note is that these substances have been found by the spectrophotometer to be nonidentical with the anthraquinones and apparently are not of that nature. Nevertheless, when an attempt is made to determine the anthraquinone content by determination of the depth of color of the ether or chloroform solution in the Lovibond Tintometer, these substances probably contribute fifty per cent of the color to the solution.

And, also, these substances having yellow color in alkaline solution, will give a tint to the red color of the alkaline solution of the anthraquinones which cannot be accurately compared with a standard alkaline solution of a pure anthraquinone.

Whether or not the anthraquinone content of a specimen of cascara bark is a measure of its medicinal value must remain a mooted question for the present. The writer is inclined to agree with statements that the "combined" anthraquinones rather than those in "free" form will furnish the basis for whatever part of the physiological activity is to be attributed to this nucleus. A recent experience with a physiologically active debitterized cascara preparation has shown the absence of any hydroxyanthraquinones, "free" or "combined." Since the yellow waxy material described herein as an impurity of the "combined" anthraquinones was found to be present in normal amount, we have been inclined to ascribe some of the physiological properties of the drug to this material or its parent substance.

The anthraquinone content of the drug may be utilized however to determine the ratio between drug and finished product, in which case it may be said that the assay has lost little of its value. A new series of investigations is called for to determine the utility of this assay process for the evaluation of bitterless cascara preparations. When we consider the time and energy that has been devoted to the examination of this drug we may be surprised to find that we have not progressed far in our knowledge of its peculiarities.

THE MICROSCOPY OF SEVERAL MANNA-YIELDING BARKS[1]

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Many species of manna-yielding plants have been tested for their saccharine exudation. Although, officially, only one variety is recognized, other members of *Fraxinus* are of economic importance. This paper gives the finding of a comparative microscopical study of the following species of *Fraxinus*, namely: *F. Ornus, F. argentea, F. excelsior, F. rotundifolia*, and a manna-yielding bark which I shall refer to as *F*. sp. "X." The latter is one of the important sources of mannite.

All five barks examined were devoid of calcium oxalate. (Oxalate crystals were found by Zimmermann in the leaf tissues of the members of *Fraxinus*.) The cork cells are similar in all the specimens, and all possessed collenchymatous cortex. The cells of the cortex differed in size, shape and thickening of walls. The most characteristic tissue is the schlerenchyma. Stone cells were present in all specimens examined, but showed marked variation in amount, location, size, pores and striations. I found secretion cavities in *F. argentea* and *F*. sp. "X". Schizogenous cavities were apparent in *F*. sp. "X" only, while in both *F. argentea* and *F*. sp. "X" lysigenous cavities were manifest. The pith parenchyma, when present, was found to be similar in all, with the exception of *F. rotundifolia*, in which case it is deeply pitted.

I therefore find that a comparison may be made between cortex, schlerenchymatous tissue, and secretion cells.

CORTEX

In *Fraxinus Ornus, F. excelsior* and *F*. sp. "X," the cells are regularly rectangular. The walls of *F. excelsior* are thicker than those of *F. Ornus* and of *F*. sp. "X." The collenchymatoused cells are less in number in *F*. sp. "X" than in *F. excelsior* and *F. Ornus*. In *F. argentea* and *F. rotundifolia* the cells of the cortex are about half as large as in the three former barks. Those of *F. argentea* are largest. Irregularity and thinness of cell walls are the outstanding features of the cortex of *F. rotundifolia*.

SCHLERENCHYMATOUS TISSUE

In *F. Ornus*, the stone cells extend from the pericycle to the cork. They are numerous, irregular in size and form, with coarsely striated and porous walls

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and pitted lumina. The stone cells of *F. excelsior* are more regularly arranged along the pericycle, smaller than those of *F. Ornus*, with lumina of the same diameter as the walls, which are finely striated and superficially pored. In *F. rotundifolia*, the stone cells are small and abundant along the pericycle. The cell walls are finely striated, non-porous with apparent cell contents. The schlerenchymatous tissue in *F. argentea* is just below the pericycle. It consists of a few stone cells, thick walled, finely striated and deeply pored. The stone cells of *F.* sp. "X" extend above and below the pericycle, but not to the cork layer. They are larger than those of *F. Ornus*, irregularly rectangular, with exceedingly thick walls which are finely striated and fissured.

Secretion cells are absent in *F. Ornus*, *F. excelsior* and *F. rotundifolia*. A summary of the tissue characteristics is given in Table 1.

TABLE 1.   THE MICROSCOPY OF SEVERAL MANNA-YIELDING BARKS.   SUMMARY

(A) *Fraxinus Ornus*	(B) *F. argentea*	(C) *F. excelsior*	(D) *F. rotundifolia*	(E) *F. sp.* "X"
Suberized tissue. Cork cells.				
Single row, small, compact cells	Single row, compact fragments	Single row, small, compact cells	Single row cells, lumina distinct	Double row cells compact
Cortex				
Regularly rectangular	Cells $+1\frac{1}{3}\times$ as large as (A), (C), and (E)	Regularly rectangular, thick-walled	Cells $1\frac{1}{3}\times$ as large as (A), (C), and (E)	Regularly rectangular, few collenchyma cells
Schlerenchymatic tissue. Location				
From pericycle to cork	Below the pericycle	Along the pericycle	Scattered but abundant along pericycle	Above and below pericycle
Stone Cells				
Irregular in size and form; walls coarsely striated and porous; lumina pitted	Rectangular; walls numerous; fine striations and deep pores; lumina small	Regularly rectangular; walls finely striated and superficially pored; lumina and walls same diameter	Small, circular, or flattened; walls finely striated and non-porous; lumina with cell contents	Irregularly rectangular; walls fine, numerous striations; pores deep; lumina very small
Secretion cavities				
Absent	Lysigenous	Absent	Absent	Lysigenous and schizogenous
Medullary rays				
Thin walled, finely pitted	Deeply pitted, walls porous	Deeply pitted, non-porous	Small cells, finely pitted; walls non-porous	Large cells, sparsely pitted; walls thin and non-porous

FIG. 1. KEY TO DRAWINGS: The microscopy of several manna-yielding barks.

	(A) *Fraxinus Ornus*	(B) *F. argentea*	(C) *F. excelsior*	(D) *F. rotundifolia*	(E) *F.* sp. "X"
1	Cork	Cork	Cork	Cork	Cork
2	Collenchyma	Collenchyma	Collenchyma	Collenchyma	Collenchyma
3	Schlerenchyma	Collenchyma (of mid. bark)	Collenchyma (of mid. bark)	Collenchyma (of mid. bark)	Cortical parenchyma
4	Pericycle	Bark parenchyma	Schlerenchyma	Schlerenchyma	Schlerenchyma
5	Parenchyma (inner bark)	Pericycle	Fibers	Parenchyma (inner bark)	Schizogenous cavities
6	Fibers	Schlerenchyma	Parenchyma (inner bark)	Pericycle	Lysigenous cavities
7	Medullary rays	Medullary rays	Medullary rays	Medullary rays	Medullary rays
8	Vessels	Parenchyma (inner bark)	Fibers	Vessels	Parenchyma (inner bark)
9		Vessels	Vessels	Fibers	
10		Lysigenous cavities	Vessels	Pith parenchyma	
11		Pith parenchyma	Pith parenchyma		
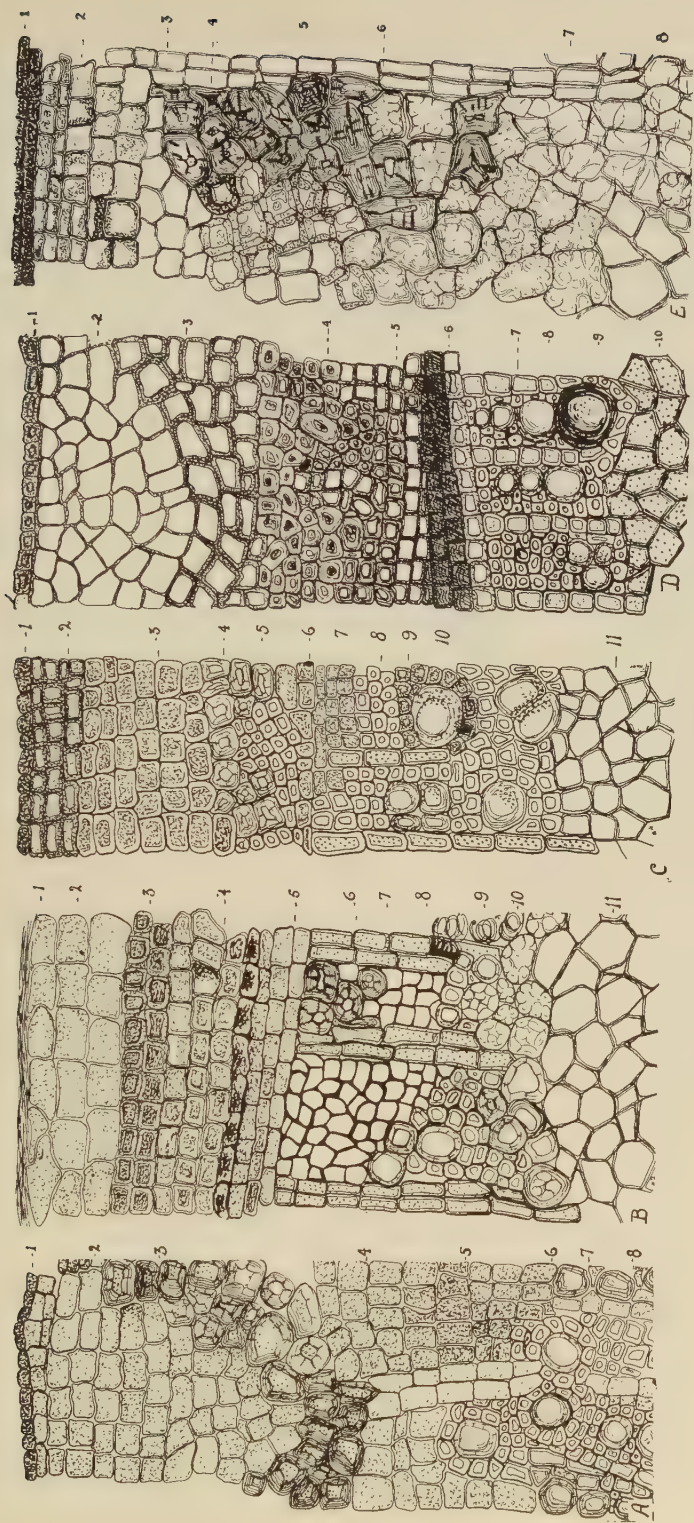
Fig. 1.

SERO-DIAGNOSTIC METHODS APPLIED TO DRUG EXAMINATION[1]

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It was my intention in my previous paper to explain my theory of sero-diagnosis in relation to experimental systematic botany, and I shall now try to illustrate to the members of the section for Pharmaceutical Botany of this International Congress the practical application of the view advanced and of the method involved.

Any important, progressive, scientific method will soon pass beyond its original limited boundaries, will soon pass from merely theoretical significance to practical application, and such will also be the case with my theory of sero-diagnosis. Originating in medicine and practically applied in that field, it has now been made of value also to pharmacy. It is my opinion that the pharmacist with his clear understanding of chemistry and chemical reactions and his ability in quantitative thinking, will all the more quickly recognize the broader relations of this work.

The possibility of replacing the methods of morphological investigation of certain details not too easily discernible by a relatively simple chemico-physiological method must evidently be of the greatest interest to the pharmaceutical botanist and pharmacognosist.

Beginning work in this direction, one must not be discouraged by the apparent complexity of the method; one must bear in mind that every chemical analysis differs from another and that necessarily a high degree of exactness is required to attain practical and definite results. Indeed, the application of sero-diagnostic methods requires the same care and the same exactness as a chemical analysis, but the routine of the former is in every case exactly the same, and with a little practice one will soon attain to a complete mastery of the technique.

Our mode of procedure may at first appear somewhat uncommon. Before we could arrive at any practical results and outline our theory, it was necessary to build upon the results and utilize the methods such as were already employed in the practical application of serum therapy in medicine, which means that experiments with the living organism had to be made, that is, with the animal body.

By introducing any protein substance into the blood stream of a living animal we always recognize more or less severe general disturbances, and especially characteristic among the symptoms are certain febrile conditions

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which are due to a pronounced toxic action of proteins generally. An eel-serum, for instance, has a toxicity one hundred times greater than that of strychnine. Powdered stone fungus (*Boletus edulis*), an edible fungus, will, if parenterally administered, promptly kill a strong, healthy rabbit in as small a dose as 0.2 mg., and similar toxicity has been established with the proteins of many other plants.

It would seem that in this toxicity of the proteins may be found reasons for the complete disintegration and destruction of these substances (their conversion to the non-toxic amido and amino forms) during digestion,—in this way protecting the body against the natural toxic irritation of food substances.

Conversely, toxic conditions (manifesting themselves by an increased temperature) are made use of in applied medicine. We are at present employing (according to Matthes) parallel to the "specific" protein therapy (tuberculin, etc.) the "non-specific" proteins in a similar manner as, for instance, evidenced by the introduction of milk (injections) in certain diseases, resulting in a complete change of the symptomatic picture, in a change to the better after a preliminary, often enormous, rise of temperature.

We explain this by looking upon the "introduced" foreign body itself as becoming the stimulus for the formation of new bodies, capable of destroying the introduced substance. These newly formed bodies are not specific, but as far as we know today, are capable of disintegrating all dead protein substances equally well. The theory is further strengthened by Abderhalden's "defense-enzyme" theory. Such "defense-enzymes" are formed or appear with certain diseases, as well as during certain specific conditions (pregnancy), and seem to function similarly to the phagocytes, that is, for the removal of dead cells.

We deal here with blood constituents, with enzymatic action, probably identical with the fibrinogen enzyme (denatured with the same temperature, reacting alike toward citrates, etc.) which in the immuno-therapy of medicine are called complements or complementary bodies (in the sense of Ehrlich's theory).

These ferments, formed either by intrinsic or extrinsic stimulation (that is, irritation either by dead protein substances present in the blood or by such proteins introduced by injection) have the property of remaining active, even after the introduction of antiseptics (1 per cent phenol), thus clearly demonstrating a purely chemical reaction of a non-living blood constituent.

By this enzymatic action of a non-specific ferment, the proteins or "albumens" (because of their toxic nature also referred to as "toxins") are then converted into "anti-toxins."

The character of the disintegrating proteins will determine the character of the resulting end-products and this fact forms the basis for the introduction of our sero-diagnostic method for the definite demonstration of the presence of unknown substances.

Forensic medicine is today making use of Uhlenhut's investigations, based upon the more definite specific serum precipitation for the determination of

blood of unknown origin, rather than depending upon the former rather uncertain microscopic method.

In food analysis the former glycogen determination method for the recognition of horse meat has likewise lost its significance and has been generally replaced by purely sero-diagnostic methods.

A similar sero-diagnostic method is also employed in the examination of fodder, as an agricultural procedure, and it is based upon numerous experiments made in our laboratory. We have no further doubt, today, that the same method is entirely applicable for the determination of drug value, both in regard to identity as well as to quality (adulterants).

Before explaining the simplest procedure, I wish to refer to some improvements of the process as generally conducted, made at out laboratory and introduced by us (cf. Mez and Ziegenspeck, Mez' Archives **12**: 1925).

After establishing our own theory as to the formation of the antitoxins (a theory materially differing from that generally accepted in medicine) it of course became necessary to demonstrate it experimentally, and this could not be demonstrated better than by substituting for the blood of living animals a serum derived from the blood of slaughtered animals, at the same time being able to eliminate the much-antagonized "vivisection" of animals. Permit me to state that our experiments were successful.

By digesting any protein substance (as, for instance, any unknown fine drug powder, which, as we know, always contains proteins) with a clear, centrifugalized serum from the blood of slaughtered animals, at 37°C, adding 1 per cent phenol solution, we will observe at first a turbidity. After a few days standing, this will either completely disappear or it may be removed after 8 days by either filtration or centrifugalization. The resulting clear serum (termed "Kunst-Serum" by us in contradistinction to a normal serum obtained from the blood of living animals) will contain the specific antitoxin.

If now we add this Kunst-Serum to an extract with 0.1 per cent NaOH or NaCl obtained from the same drug from which the above Kunst-Serum was prepared we shall notice after a short time (average observation time 12 hours) a white, flocculent separation, which, however, will not show if the protein solution used is not of the same type.

Upon these reactions we have based our extensive "Koenigsberger phylogenetic tree" which may also be utilized for practical drug identification.

Full directions for the working methods will be found in the paper of Mez and Ziegenspeck, previously mentioned.

I especially beg to emphasize that these methods (a patent has been applied for in Germany) promise to become of the utmost importance in medicine. We know, for instance, of the anaphylactic conditions resulting from the administration of horse-sera in diphtheria to patients having an idiosyncracy towards serum (which as we know is the basis for diphtheria antitoxin). In such cases our Kunst-Serum of diphtheria bacilli (which could also be made from human blood) will be particularly helpful.

Furthermore, since one has a better control over the titer in the manufac-

ture of the Kunst-Serum, it will of course be considerably easier to grade efficiency, that is, to prepare stronger or weaker sera.

In like manner, our method promises to become of extreme importance in treatment of snake-bites (in tropical countries) since it affords a means of digesting these poisons *in vitro* with sera obtained from the dead animal. We anticipate the possibility of exact dosages and thereby of inevitable cures.

Concluding, I wish to say that, if one does not fear the trouble of investiggating our only apparently complicated method (actually a very simple procedure) one will find that it enables us clearly to recognize and to determine vegetable substances, even when in practically unrecognizable condition.

In this manner, moreover, we clearly demonstrate the basic uniformity of all biological science and offer here a method, originally investigated in medicine elaborated and utilized in theoretical botany, which now promises to become of similar importance and value in applied botany, that is, in pharmacognosy,

TAXONOMY AND PHARMACOGNOSY OF THE GENUS APOCYNUM[1]

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All pharmacognosists engaged in taxonomic work must realize the short-comings of the present systems of botanical classification as represented by the diversities in the analytical keys appearing in works on the flora of various regions. These keys must be sufficiently elastic to allow for slight natural variations in plants of a given species but must also be adequate to differentiate between closely related species. It is often a difficult problem to decide if slight variations from type form are within reasonable species range. Undoubtedly the wisest procedure from a taxonomic standpoint lies in the happy medium between considering even the slightest variation from type form or description as justification for new specific titles and the equally objectionable alternative of lumping all slightly differing forms as varieties of a single species. The first extreme results in too many species with almost imperceptible shades of difference between them, and the second tends toward the same result, merely substituting varieties for species. In the first instance too great value is attached to fine distinctions, while in the second, slight but constant differences are passed over.

For the pharmacognosist the problem of botanical identity is further complicated by the fact that he may be required to deal with the medicinal part of the plant, and in many instances this part is not accompanied by the flowers, fruits, and leaves upon the morphology of which our whole structure of systematic work is based. A correlation of taxonomic characters with histological structure would be helpful to both the taxonomist and the pharmacognosist, but comparatively little has been accomplished along these lines. It is not to be expected, nor is it desirable, that histological data should supplant morphological evidence in taxonomy, but the possibilities of coordinating the two are worthy of consideration.

This investigation was undertaken at the suggestion of Dr. H. H. Rusby and is the second of a series dealing with the morphology and comparative histology of the members of different genera. In a previous research upon the morphology and histology of twenty-two species of *Erythroxylon* ("Structural variations in *Erythroxylon* leaves." Jour. Amer. Phar. Assn., Vol. **15**:), three broad propositions were offered as worthy of further investigation. These were stated as follows:

(1) Histological characters of the different species in a given genus, while

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showing a certain degree of agreement also show differences characteristic of the individual species.

(2) The histological characters of a given species are sufficiently constant to warrant the admission of this evidence in systematic work.

(3) In instances of doubt regarding specific or variational rank, histological data should be given equal value with morphological evidence in determination.

These propositions were stated as a basis for future research along similar lines and not with any idea of their being established facts, even though they held good in the investigation of the several species in the genus *Erythroxylon*. As the acquisition of fresh and flowering material was impossible in the study of the Erythroxylons, attention was necessarily restricted to leaf characters. In the present work flowering material was readily available, so that a more comprehensive study is possible. The genus *Apocynum* was purposely selected not only because material could be readily secured but also because of the unsatisfactory treatment of this genus in systematic work. The studies of Edw. Lee Greene are probably the most accurate. Miller's descriptions, although based upon the examination of a vast collection, are too general. Britton's work follows with greater accuracy but with considerable abbreviation. The latest edition of Gray's Manual shows a reversion in that several species recognized by other authorities are merely accorded varietal rank. None of the authorities considered any other evidence than the superficial characters commonly used in taxonomy. Although intimately concerned with the pharmacognosy of *Apocynum*, N.F., the problem is broader than the possibility of establishing pharmacognostic differences in the rhizomes of the several species.

The materials used in this study were collected and identified by Dr. Rusby and myself. In five instances the entire flowering plants were secured so that there might be no question as to the botanical identity of the rhizomes. The keys of Gray and Britton were used in the taxonomic work. The species examined were—*Apocynum cannabinum* L.; *Apocynum album* Greene; *Apocynum hypericifolium* Ait.; *Apocynum pubescens* R. Br.; *Apocynum urceolifer* G. S. Miller, and an herbarium specimen of *Apocynum androsaemifolium* L.

Taxonomy

This part of the study consisted in the comparison of the collected material with the descriptions appearing in "Gray's Manual of Botany," 7th edition, and Britton's "Manual of the Flora of the Northern States and Canada." All specimens were further compared with herbarium materials both at the College of Pharmacy and at the New York Botanical Garden. In addition to the usual procedure, an examination of the flowers under a magnification of 26× was made as the information gained thereby, particularly with reference to the form of the stigma and the basal portions of the thecae, may be of no little importance in deciding doubtful forms.

Apocynum cannabinum L. This specimen was obtained from the New York Botanical Garden. In taxonomic characters it agrees closely with the description in Britton's "Flora." The stigma is approximately 0.5mm. long and 0.25mm.

wide. The upper portion is rounded and two-cleft. The middle part, to which the anthers are attached, is the widest, but the zone of adherence is narrow (Fig. 1, A). The stamens average 1.5mm. in length and 0.5mm. in width. The basal portions of the thecae are long and sharp pointed but the inner edge of each theca is straight, curvature to the point being along the outer edge only
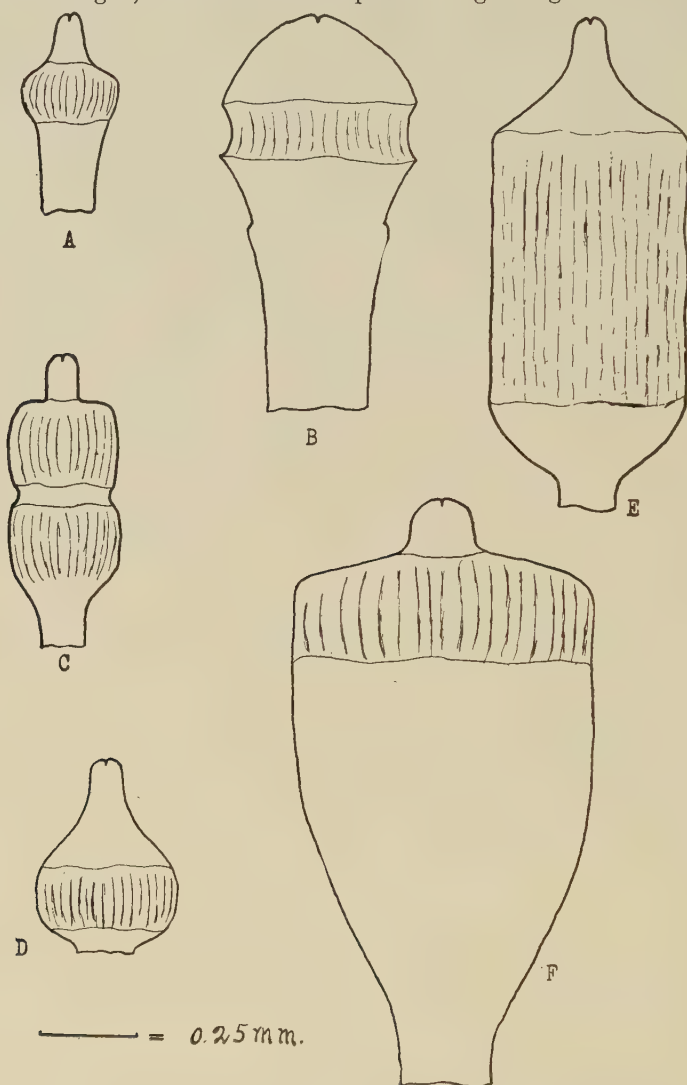
Fig. 1. Forms of the stigma in *Apocynum*. A, *Apocynum cannabinum* L.; B, *A. album* Greene; C, *A. hypericifolium* Ait.; D, *A. pubescens* R. Br.; E, *A. urceolifer* G. S. Miller; F, *A. androsaemifolium* L.

(Fig. 2,A.). The corolla is about 2.75mm. in height and the lobes are coherent for about one-half this distance.

Apocynum album Greene. This and the three following species were collected in northern New Jersey. It agrees substantially with Britton's description

except that the larger leaves subtending axillary branches and the very small leaves subtending the cymes are almost sessile. The specimen disagrees with the description in "Gray's Manual" in that it is not dwarfed, although diffuse and with narrow leaves. The stigma is approximately 1.0mm. long and 0.5mm. wide. The upper portion is broadly curved and slightly two-cleft. The middle part, to which the anthers are attached, is no wider than the top and the zone of adherence is narrow. From this point the stigma gradually narrows into a short style (Fig. 1, B). The stamens are about 2.0mm. in length and about 0.5mm. in
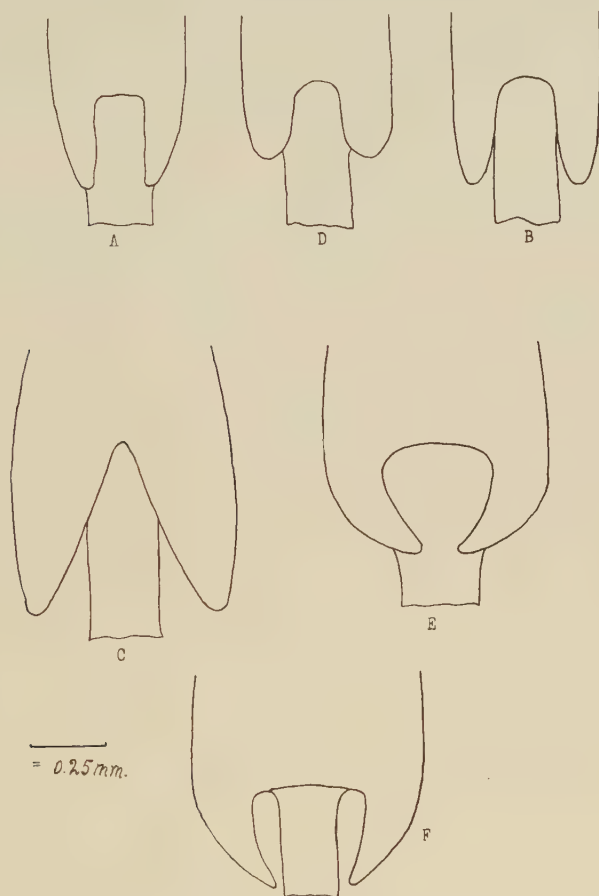
Fig. 2. Basal lobes of the thecae in *Apocynum* A, *Apocynum cannabinum* L.; B, *A. album* Greene; C, *A. hypericifolium* Ait.; D, *A. pubescens* R. Br.; E, *A. urceolifer* G. S. Miller; F, *A. androsaemifolium* L.

width. The basal portions of the thecae are long and sharp pointed with curvature along both inner and outer edges (Fig. 2, B). The corolla is about 1.75mm. in height and the lobes are coherent for about one-half of this distance.

Apocynum hypericifolium Ait. This specimen, although differing in certain respects from the descriptions of both Britton and Gray was more in accord with

their specifications for this species than with any of the others enumerated in these volumes. It was therefore provisionally identified as *A. hypericifolium*. The points of difference from the descriptions are that the leaves show a slight pubescence and the calyx segments are longer than the corolla tube. Whether or not these differences are sufficient to warrant naming the specimen as a new species is very doubtful. The stigma is approximately 0.75mm. in length and 0.25mm. in width. The upper portion is small, rounded and two-cleft. The middle portion is somewhat cylindrical but with a constriction at about the center. There appear to be two attachment zones for the anthers, one above and one below the constriction (Fig. 1, C). The stamens average 2.25mm. in length and 0.75mm. in width. The basal portions of the thecae are long and sharp pointed with the inner edges forming an acute angle below the insertion of the filament (Fig. 2, C). The corolla is about 3.0mm. in height and the cohesion extends about one-half this distance.

Apocynum pubescens R. Br. This specimen agrees with the descriptions in Britton and Gray exception that the leaves are not as densely pubescent as one would imagine from the descriptions. The stigma is approximately 0.5mm. long and 0.25mm. wide. The upper portion is rounded, two-cleft, and the organ gradually broadens to the base. The base is the largest part and the stamens are adherent at this point (Fig. 1, D). The stamens are about 1.75mm. in length and 0.5mm. in width. The basal portions of the thecae are rather short and with rounded extremities (Fig. 2, D). The corolla is about 3.25mm in height and the cohesion extends about two-thirds of this distance.

Apocynum urceolifer. G S. Miller. This specimen offered considerable difficulty in identification and in distinction from herbarium specimens of *A. Milleri* and *A. medium*. The flowers ranged from companulate to urceolate, with calyx segments shorter than the corolla tube. The leaves show perciptible indications of trichomes and are almost entirely of ovate-lanceolate form. This similarity to both *A. medium* and *A. Milleri* is commented upon in both Britton and Gray and the descriptions given are not satisfactory. The stigma is approximately 1.5mm. in length and 0.5mm. in width. The upper portion is rounded and two-cleft. The middle portion forms the bulk of the organ and is almost cylindrical with a very wide attachment zone for the anthers. From this point it abruptly curves into a very short style (Fig. 1, E). The stamens average 2.5mm. in length and 0.75mm. in width. The basal portions of the thecae, while long and sharp pointed, are incurved in such a manner as to extend part way across the underlying filament (Fig. 2, E). The corolla is about 5.0mm. in height and the cohesion extends about three-fourths of this distance.

Apocynum androsaemifolium L. This material was obtained from a herbarium specimen at the School of Pharmacy, Columbia University, and it agrees in all respects with the printed descriptions. The stigma is approximately 1.5mm. in length and 0.75mm. in width. The upper portion is small, rounded and two-cleft. The organ abruptly widens and the middle part is cupulate with a narrow adhesion zone at the upper end. This middle portion gradually narrows to a short style (Fig. 1, F). The stamens average 3.0mm. in length and 0.75mm.

in width. The basal portions of the thecae are sharp pointed and slightly curved toward and over the underlying filament (Fig. 2, F). In general, the stamens of this species are larger than the others examined. The corolla is about 6.0mm. in height and the cohesion extends about two-thirds this distance.

HISTOLOGY AND PHARMACOGNOSY

In this part of the work first consideration was given the gross or macroscopic characters of the rhizomes and roots of the five species collected. After this, attention was turned to the histological characters of the rhizomes and leaves. Several commercial samples of *Apocynum cannabinum* and the bitter root supposedly from *A. androsaemifolium* were examined. As the botanical identity of these materials may be open to question, more confidence rests in the examination of the five specimens secured in fresh condition.

Gross Characters of the Rhizomes. In all of the specimens both vertical and horizontal rhizomes were present in varying proportions but as the depth of the horizontal rhizome from the surface is probably dependent upon soil conditions, little dependence can be placed upon this character.

Apocynum cannabinum. These rhizomes and roots range up to 8mm. in diameter and are straighter than any of the other species. The surface shows well defined ridges and is grayish-brown in color. The pith region of the rhizome is large and comparatively few rootlets are present.

Apocynum album. These rhizomes and roots range up to 5mm. in diameter. The surface shows many prominent ridges and is grayish-brown in color. The pith region of the rhizome is large and in general the specimen shows a great similarity to *A. cannabinum.* Rootlets are only apparent on the smaller roots.

Apocynum hypericifolium. These rhizomes and roots range up to 15mm. in diameter. The surface is but slightly ridged and is dark brown in color. The pith region of the rhizome is small and numerous fine roots and rootlets arise from both the rhizome and main roots.

Apocynum pubescens. These rhizomes and roots range up to 10mm. in diameter. The surface is irregularly furrowed and of light brown color. The pith region of the vertical rhizomes is large but is much reduced in the long horizontal rhizomes. Both rhizomes and roots are much branched and numerous fine rootlets are present. In point of weight this is the lightest rhizome of the entire series.

Apocynum urceolifer. These rhizomes and roots seldom exceed 5mm. in diameter. The surface is but slightly ridged and is a light reddish-brown color. The pith region of the rhizome is very small and both rhizomes and roots show a greater degree of xylem development than the others of the series. The roots and rhizomes are tortuous and give rise to very few rootlets.

Histological Characters of Rhizomes. Sections of the rhizomes of the five specimens showed great similarity as regards general structure. The cork zone consists of five to ten layers of light brown, tangentially elongated cells. The cortex is parenchymatic with numerous irregular latex channels. Stone cells occur in this region in the following species—*A. urceolifer, A. hypericifolium*

and *A. pubescens*. Current literature notes the presence of stone cells in the rhizome of *A. androsaemifolium* in distinction to their absence in *A. cannabinum*, and none of the samples of *A. cannabinum* showed stone cells, notwithstanding the National Formulary specification of "few or none." The phloem region shows but little traces of fibrous tissue. The xylem zone is extremely large as compared with the phloem. The pith region in most species is fairly well marked and may contain small numbers of latex channels. Stone cells also occur in the pith of *A. androsaemifolium*.

The only histological elements which might be of service in the identification of species are the stone cells occurring in the cortical region of the four species named. It may be noted in passing that, although the presence of stone cells is not a sure indication that an *Apocynum* belongs to the androsaemifolium series, in all specimens of this series in which stone cells were found, they were plentiful, and they were located in all parts of the cortex, especially toward the cork layer. In those specimens of the cannabinum series containing stone cells these elements were near the sieve, with none in the outer cortical layers. It is also worthy of note, especially in view of the fact that the present National Formulary description states that stone cells are few or absent, that the latter elements were absent in every sample of *A. cannabinum* examined.

Histological Characters of the Leaves. Sections of the leaves of the five species show a similarity in structure which, aside from the presence of trichomes in certain species, renders histological differentiation of species difficult or uncertain. The lower epidermal cells of all species bear well developed papillae. Unicellular and uniseriate trichomes occur on the lower surface of *Apocynum pubescens*, *A. urceolifer*, *A. hypericifolium* and *A. androsaemifolium*. These trichomes range from one to six cells and their surface is papillose.

Summary

Although this investigation has not shown a clear line of histological characters correlated with the taxonomic features of the genus, the following facts have been brought to light:

1. The size and form of the stigma and the point of attachment between stigma and stamens differs in different species.

2. The form of the basal lobes of the thecae differs in different species.

3. The size and more especially the relative cohesion of the corolla lobes varies in different species.

4. Stone cells occur in the cortex of the rhizome in *A. urceolifer*, *A. hypericifolium* and *A. pubescens* as well as in *A. androsaemifolium*.

5. The leaves of *Apocynum urceolifer*, *A. pubescens* and *A. hypericifolium* bear well developed trichomes.

6. *Apocynum album* and probably *A. hypericifolium* would conform to the National Formulary description for *Apocynum cannabinum*.

A PROPOS DE L'ESPECE EN BOTANIQUE[1]

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Malgré toutes les autres questions soulevées par l'étude des phénomènes de la vie végétale, la spécification reste à la base des recherches scientifiques botaniques. Pour une étude sérieuse de la Morphologie, de l'Anatomie, de la Cytologie, de la Physiologie et de la Biologie végétale, comme d'ailleurs pour ces mêmes recherches dans le domaine animal, il sera toujours nécessaire de connaître la position systématique de l'objet à mettre en expérience ou de pouvoir au moins la fixer durant le cours ou à la fin des expériences.

Malheureusement la définition spécifique d'un organisme vivant est loin d'être aisée et nous admettons, sans la moindre hésitation, que des caractères anatomiques, cytologiques, physiologiques et biologiques peuvent et doivent intervenir dans la spécification.

Nous estimons donc qu'il convient dans l'intérêt d'une connaissance mieux définie des organismes vivants de soutenir et de pousser très largement des recherches dans ces diverses directions.

Mais avant d'obtenir, grâce à ces appoints, une synthèse capable de nous faire mieux concevoir l'espèce, il faut cependant être parti d'un type désigné "spécifique" sur lequel devront être basées toutes les expériences. C'est la raison pour laquelle, ainsi quelle soutient A. De Candolle, la systématique aura toujours sa très grande importance; elle se trouve à la base et à l'aboutissement de toutes les études scientifiques biologiques.

Il est indiscutablement aisé de dire ce que doit être l'espèce; mais il est beaucoup moins aisé d'appliquer la définition spécifique car les organismes vivants se laissent bien rarement englober dans un schéma.

Certes pour être caractérisé de "spécifique" on peut admettre que l'organisme doit se reproduire semblable à lui-même; bien entendu il ne faut pas accorder au terme "semblable" une trop grande rigidité, car certainement la variation existe sur un même plant et dans la descendance, en outre des faits de mutations paraissent incontestables.

Il faut cependant admettre que si la descendance est loin d'être conforme aux parents, il faut la considérer plutôt comme due à une origine hybride; et il ne serait même nullement impossible que les mutations soient dues en définitive à un trouble amené chez ces plantes à la suite d'une hybridation.

Mais de la concordance des descendants et des parents, on ne peut déduire que tout organisme qui se reproduit semblable à lui-même constitue toujours un type spécifique au sens taxonomique du mot, car les variétés, les formes

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peuvent, si les conditions biologiques restent égales, donner des descendants conformes aux ascendants. Car pousser cette caractéristique serait indiscutablement tomber dans la spécification de l'individu, aller même plus avant encore que les "Jordaniens."

L'espèce se réduirait dès lors à un des éléments de l'ensemble spécifique. On a cru aussi parfois pouvoir donner comme critère de l'espèce qu' "elle est toujours capable de se reproduire," différant en cela des hybrides qui seraient stériles.

Si cette conception paraît exacte pour certains types spécifiques, en particulier dans le règne animal, elle ne paraît pas pouvoir être appliquée dans le règne végétal où des hybrides, même bi- génériques, sont indiscutablement féconds. On pourrait certes discuter sur la valeur des genres entrant dans la constitution de ces hybrides, mais il n'en est pas moins certain que les graines obtenues par la fusion des masses polliniques et des ovules d'organismes végétaux bien différents sont viables.

L'hybridation a d'ailleurs d'après nous joué un rôle très considérable dans la constitution de ce que nous sommes amené à dénommer actuellement espèce.

Cette hybridation a, pensons-nous, joué dans la création de formes végétales un rôle beaucoup plus actif que l'adaptation, le sélectionnement et le sport, et nous n'hésitons pas à déclarer que bien des "espèces" décrites dans les Flores seraient, d'après nous, à ranger dans la catégorie des hybrides si la culture pouvait en être tentée. Elles nous montreraient, dans la descendance, l'apparition de formes différentes dont certaines pourraient, fort probablement, être rapportées aux plantes ancestrales.

Nous citerons ici un exemple. Nous avons décrit dans le temps un *Solanum Sapini* du Congo; il présentait un ensemble de caractères qui le différenciait des autres types africains connus à cette époque. Notre ancien élève et ami A. Sapin avait, en même temps que des spécimens d'herbier, recueilli des fruits et des graines de sa plante, et il nous fut possible grâce à cet envoi de tenter la culture de sa plante au Jardin botanique de Bruxelles. Nous fûmes très surpris de voir les semis de ces graines donner naissance à deux formes très différentes: l'une très épineuse, l'autre totalement privée d'épines. Les deux plantes dérivées du semis appartiennent donc chacune à l'un des deux groupes proposés par M. Wright dans sa révision monographique du genre *Solanum* pour le "Flora of tropical Africa."

Les conclusions très nettes de notre observation étant donc que le *Solanum Sapini* devait être considéré comme hybride, et que le caractère tiré des épines doit être considéré comme très suspect au point de vue de la classification des espèces, M. H. Burkill, du Kew Herbarium à qui nous avons, sur sa demande, envoyé des documents de nos plantes encore en culture, admet qu'elles doivent être rapportées au *Solanum macrocarpum* subspec. *S. Sapini* (Kew Bull. 1925 p. 339), formée par une hybridation entre *Solanum duplosinuatum* Klotzsch, épineuse et une forme qui pourrait être, ou ne pas être, *S. macrocarpum* L., dans lequel d'après M. le Dr. G. Bitter on rencontrerait des variétés épineuses ou inermes.

Beaucoup de plantes rencontrées cultivées, subspontanées ou même à l'état sauvage sont pour nous, comme le *Solanum Sapini*, des descendants d'hybridation. Cette origine plus fréquente que beaucoup veulent l'admettre complique grandement la question systématique; il est en effet bien difficile de reconnaître par des caractères morphologiques, par des caractères "intermédiaires," un hybride d'un type spécifique.

La cytologie, par l'étude chromosomique du noyau semble devoir donner un moyen plus précis de distinguer les deux catégories d'organismes. Mais pour être vraiment pratique l'étude cytologique, comme les recherches anatomiques, devrait pouvoir mettre en relief des corrélations entre les caractères anatomiques, ou nucléaires et ceux d'autres organes de la plante, car l'étude du noyau ne pourra être faite dans tous les cas, et sans caractères correlatifs il ne sera nullement plus facile sur des caractères anatomiques ou chromosomiques de définir avec certitude une espèce.

Certes la culture pourra nous aider dans bien des cas, mais elle non plus ne peut toujours être faite. Il ne sera pas possible par exemple de juger de la descendance de bien des plantes ligneuses; la vie d'un homme ne suffirait pas à la définition des espèces de ce groupe de végétaux dont la croissance est souvent très lente, et chez lesquels la floraison et la fructification sont soumises à des aléas nombreux.

Par des études poursuivies durant des années les systématiciens sont arrivés à la notion que l'espèce présente des caractères, en particulier morphologiques, variant dans une certaine mesure; mais l'amplitude de ces variations est loin toujours été précisée.

Si les caractères morphologiques externes que nous cherchons à utiliser se montrent variables, et ne peuvent aux dires de beaucoup servir à la différenciation des espèces, les chromosomes, nous y avons fait allusion déjà, auxquels on voudrait depuis peu, plus souvent recourir ne subissent ils pas eux aussi des variations? Il semble que oui! La variation chromosomique serait donc, elle aussi à étudier!

De ce fait indéniable, qu'un type actuellement défini "spécifique" peut varier, on a conclu parfois qu'il fallait bannir de la notion de l'espèce toute idée de constance absolue des caractères!

Nous ne sommes pas totalement de cet avis, car si nous ne voulons nullement nier,—nous serions très porté à fournir à ce sujet des éléments positifs dans la discussion,—la variabilité d'un grand nombre de caractères des types "spécifiques," nous estimons qu'il doit exister pour les véritables espèces un ou des caractères qui persistent, malgré toutes les modifications extérieures, un caractère vraiment constant!

Ce caractère ou ces caractères, d'après nous primordiaux, ne sont probablement pas très apparents et ce serait la raison pour laquelle ils n'ont pas pu être mis en vedette, ou ils se trouvent noyés dans toute une série de caractères sur lesquels ont porté plus spécialement notre attention et nos études.

Nous admettrions donc la variation de tous les caractères d'un organisme, sauf de celui qui doit être considéré comme "spécifique" au sens propre. Si ce

dernier caractère se trouve dans des conditions telles qu'il ne peut se maintenir sans devoir être transformé profondément, nous pensons que l'espèce doit disparaître. Ainsi auraient disparu les anciens types, ainsi s'en vont sans se modifier profondément des types spécifiques à l'évanouissement desquels nous assistons dans l'analyse des Flores des régions tropicales soumises à l'action intensive de l'homme, et même dans celle des Flores de nos régions tempérées où la civilisation modifie considérablement le tapis végétal.

Si, nous l'avons dit, il faut actuellement encore considérer les caractères externes, morphologiques, comme intervenant surtout dans la définition spéci-fique, nous pensons que des études approfondies dans les autres branches des sciences biologiques permettront un jour de mettre en relief des corrélations entre caractères morphologiques, anatomiques, cytologiques et biologiques.

Nous serons alors à même de spécifier, sans contestation possible, des orga-nismes, car nous aurons pu définir lesquels de ces caractèressont restés im-muables.

M. le Prof. Gravis, dans un discours à l'Académie des Sciences de Belgique,[2] avait au sujet de la spécification en sciences naturelles amené la conclusion que dans la pratique il y avait lieu de désigner sous le nom d'espèce "Les groupes linnéens et ceux de valeur égale constitués plus récemment."

Cela peut valoir théoriquement!

Mais comment pourrons nous définir un groupe linnéen, et sur quelles bases établirons nous les groupes de valeur égale.

Les plantes que l'immortel Linné a eues en vue dans ses descriptions, reprises souvent dans les travaux de ses prédécesseurs, et qu'il considérait lui-même souvent comme des plus difficiles à définir, sont elles même très inégales! Très souvent d'ailleurs le grand phytographe a eu affaire seulement à des formes relativement éloigneés des types que des recherches plus modernes ont mis en évidence.

Il n'y aurait donc aucune nécessité de conserver toute espèce linnéenne; il n'y aurait aucune bonne raison, à notre avis, de ne pas placer, dans certains cas, un nom linnéen franchement en synonymie, lorsque ce nom correspond à une variation d'une plante décrite portérieurement comme type.

L'erreur est humaine, et il n'y a aucune raison de maintenir des erreurs avérées!

On pourrait se figurer que dans la flore de nos régions tempérées les espéces, parce qu'elles sont peut être plus spécialement du type "linnéen" sont mieux définies que dans la flore des pays neufs. Il n'en est rien et l'étude approfondie de nos flores d'Europe montre à chaque pas la fausseté de nos jugements.

La variation dans l'appréciatios des espèces, surtout dans celles de nos plantes européennes, a fait jeter le discrédit sur la systématique par les ana-tomistes, cytologistes, biologistes, qui reprochent aux systématiciens et mono-graphes d'encombrer inutilement la science par des descriptions non compa-rables, trop étendues et par la création d'un nombre considérable de binomes spécifiques, origine d'une vaste synonymie.

[2] Gravis, A. La morphologie végétale. Bull. Acad. roy. Belgique Cl. des Sciences, n°12, 1920.

Un de nos confrères en sciences naturelles, le Prof. Lameere, a dit un jour dans le discours d'ouverture du premier Congrès international d'entomologie "Les descriptions isolées et surtout non comparatives, devraient être absolument proscrites; l'heure est venue de coordonner."

Certes nous sommes tout à fait d'accord avec lui qu'il faut chercher à décrire avec soin les types spécifiques et à en donner des descriptions plus comparatives, mais nous ne pensons pas que dans le domaine de la botanique il soit possible d'éviter, d'ici longtemps, la publication de descriptions isolées et par suite à plus forte raison, pour tous les genres en général, de coordonner, de faire somme toute oeuvre de synthèse.

Il faudra au contraire, pensons-nous, encore pendant fort longtemps fournir des analyses fouillées; elles nous démontreront, si nous les construisons avec soin, le peu de valeur de synthèses basées sur une documentation encore beaucoup trop peu complète, tant au point de vue du matériel spécifique, du nombre des espèces que de la connaisance de leurs caractères.

Des diagnoses sans valeur ont certes vu le jour, et sans conteste bien des descriptions jusqu'à un certain point inutiles apparaîtront encore dans les littératures systématiques botanique et zoologique; mais ne se produit-il pas dans d'autres branches de la science botanique des travaux sans valeur ou de peu d'utilité! On ne peut, de tels faits, tirer argument contre une branche de l'étude des sciences naturelles contre la Systématique!

Il y a, en outre, lieu de faire remarquer que si dans certains cas il y a synonymie complète entre des créations nouvelles et des espèces plus anciennes cette synonymie peut être le résultat d'une erreur non imputable directement à l'auteur le plus moderne. Les descriptions anciennes sont très souvent particulièrement incomplètes, les documents d'herbier, sur lesquels on a cru pouvoir s'appuyer, de définition souvent différente.

Disons en outre que dans la plupart des cas cette synonymie n'est pas totale, les descriptions nouvelles ont souvent l'intérêt de faire ressortir des caractères dont le premier auteur n'avait pas cru devoir parler ou qu'il n'avait pas observé sur les documents étudiés, ces caractères n'étant pas présents. La multiplicité des descriptions, qui a donné naissance à la synonymie, a donc provoqué des recherches de la part des systématiciens et son résultat a été en définitive celui vers lequel nous devons tendre: changer nos données provisoires en données se rapprochant de plus en plus de la réalité, par conséquent de faire de mieux en mieux connaître le groupe d'organismes que nous dénommons "espèce," de lui donner une description de plus en plus précise, de plus en plus complète.

La création de synonymes est, estimons-nous en général, impossible à éviter, et nous la considérons comme une nécessité des progrès de la Science. Il sera d'ailleurs toujours plus utile de décrire des organismes sous un vocable nouveau, quand on se trouve dans l'impossibilité de prouver leur identité avec des organismes plus anciennement connus, que de les rapporter sans preuves totales à ces types anciens. On risque par ce procédé d'assimilation souvent aisé, de devoir un jour morceler le type composite, et de devoir employer dans la

désignation des organismes le néfaste "pro parte", beaucoup plus embrouillant que la synonymie simple.

Nous devons je pense,—bien peu de naturalistes seront opposés à notre manière de voir—, admettre qu'une espèce, n'est pas dans les conditions actuelles, dans l'état provisoire et transitoire de nos connaissances, à définir par un caractère unique. Nous devons pour affirmer la spécification recourir encore à une série de caractères, constituant par leur ensemble les "caractéristiques" de l'espèce.

M. Boulenger a vivement insisté sur cette situation dans la suite des études qu'il a publiées sur les Roses de l'Herbier Crépin (Bulletin du Jardin botanique de Bruxelles), et nous ne voulons nous appesantir davantage sur ce sujet.[3]

Il nous paraît donc indiscutable que bien des caractères actuellement proposés par les monographes, sont sujets à varier, et utilisés seuls ils ne peuvent permettre une spécification définitive. On peut se demander, vu l'état actuel de nos connaissances, sur quels organes doivent porter les caractères spécifiques? Cette question a été bien souvent posée et malheureusement il n'a jamais pu y être répondu d'une façon précise! Il nous parait bien certain que des caractères de même genre ne peuvent être utilisés pour la distinction des espèces appartenant à tous les groupements familiaux de végétaux.

Si nous pouvions employer, comme en chimie, des réactions partout les mêmes, la définition serait beaucoup plus aisée, mais l'organisme vivant ne peut être enfermé dans une formule mathématique!

Si, dans certains cas, les caractères tirés des organes foliaires peuvent nous paraître excellents, et permettent une classification relativement aisée de bien des types végétaux, dans d'autres cas il ne peuvent nous être d'aucune utilité dans la spécification.

D'autres ont estimé que les caractères floraux avaient une valeur prépondérante, mais combien de fois n'a-t-on pas démontré la variation de certains caractères floraux sur le même pied durant la même année ou dans des années successives!

On a considére aussi les fruits et les graines comme fournissant des caractères de toute première valeur; mais là aussi la valeur est loin d'être constatée. Dans certains groupes ces organes sont d'une très grande uniformité, dans d'autres groupes ils présentent au contraire des variantes considérables du moins entre espèces très voisines pour d'autres caractères, de telle sorte qu'il ne peut être tablé sur eux d'une manière générale.

L'hypothèse mise en avant par certains théoriciens, qu'il faudrait appliquer pour toute les classifications végétales la même méthode ne peut être prise en considération.

Nous sommes cependant, dans le but de faciliter les recherches, pour reconnaître les types les uns des autres, forcé d'utiliser des sortes de "clefs analytiques" dans lesquelles nous essayons de placer, en opposition, des caractères faciles à

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[3] Boulenger, G. A.   Les Roses d'Europe de l'Herbier Crépin.   Bull. Jard. Bot. Bruxelles **10** (fasc. 1): 1924.

mettre en évidence, et autant que possible peu de caractères de façon à faciliter l'examen.

Mais on ne peut de ce fait reprocher au botaniste descripteur de se baser pour la distinction des espèces sur un caractère que d'autres considèrent de peu d'importance et de valeur secondaire. Rappelons que tout descripteur consciencieux considère de telles clefs comme "un moyen" pour amener à une approximation; ce moyen est provisoire et souvent, il le sait, artificiel, et jamais il ne dispense le chercheur de comparer avec soin la plante à l'étude, à la description originale et à celles qui ont été refaites postérieurement.

Ne faisons donc dire à ces clefs ce qu'elles ne peuvent dire! Si, souvent, elles peuvent servir à classer les espèces en groupes dont les représentants paraissent voisiner, il ne faut pas tirer de cet apparentement, souvent très superficiel, un apparentement indiscutablement généalogique.

Si dans un même genre on utilise par exemple pour établir des clefs analytiques deux caractères différents; les clefs amèneront à des groupements d'espèces loin d'être comparables.

Nous pourrions à ce sujet citer bien des exemple, nous en prendrons un dans les études que nous avons entreprises récemment sur les *Uapaca* types africains de la grande famille, très polymorphe, des Euphorbiacées.

Les espèces du genre *Uapaca* à fleurs dioïques sont encore très mal connues; un grand nombre de leurs représentants n'existent dans les herbiers que sous la forme femelle ou la forme fructifère; et il est en outre bien des cas, dans lesquels il est très difficile d'affirmer, sans le moindre doute, que des échantillons à fleurs mâles et à fleurs femelles sont à rapporter à un même type spécifique.

En présence de cette difficulté nous avons été amené à essayer le classement des matériaux en utilisant deux clefs analytiques, basées l'une sur les fruits et en particulier sur leurs pyrènes, l'autre sur les feuilles et nous sommes arrivés comme nous le pensons à un groupement totalement différent.

Cela nous semble la preuve que ces clefs,—utiles—, ne peuvent être considérées comme tranchant toutes les difficultés; elles nous fournissent des résultats provisoires; des études ultérieures, basées sur de nouveaux documents de plus en plus complets, les feront indiscutablement modifier et améliorer.

Il convient également de noter à propos de ce genre que nos observations récentes font voir que non seulement nous sommes peu avancés dans la connaissance des espèces, mais que les caractéristiques génériques sont également fort peu nettes.

Nous trouvons en effet dans la diagnose générique du genre *Uapaca*: ovaire 2-4-loculaire, trigone; coques du fruit à 2-1 graines.

Un ovaire 2-loculaire ou 4-loculaire, comme un fruit biloculaire ou 4-loculaire, ne pourrait guère être trigone, à moins de considérer dans ce fruit une disposition tout à fait irrégulière des loges, et de fait dans les fruits à 4 loges,—dans les cas observés à 4-pyrènes—, nous trouvons un ensemble nettement arrondi, les 4 loges disposées très régulièrement en croix.

Si la définition concordait avec la réalité il faudrait que les fruits 2-3 ou 4-

loculaires renfermant 2 graines par loge, continenent 4-6-8 graines ou par suite d'avortement d'un des ovules, 2-3-4 graines.

Nous avons étudié des ovaires 3-gones, à 3 loges, à loges 2-ovulées, les fruits, paraissant correspondants, sont à 3 loges uniseminées. Nous avons également étudié des fruits à 4 graines, des fruits à 5 et à 6 graines, toujours régulièrement disposées autour du centre, et dans ces fruits, à l'état adulte, il n'y avait pas trace d'avortement.

Il y a donc lieu de recherche l'explication de cette anomalie déjà dans la structure de l'ovaire des fleurs femelles. Le nombre de loges pourrait être un caractère nettement spécifique; comme il pourrait aussi être le résultat de croisements entre types différents ayant amené dans la constitution des ovules des modifications notables.

Nous basant sur des caractères foliaires, comme l'a fait déjà M. Hutchinson dans le "Flora of tropical Africa" nous constituons par notre clef des groupements dans lesquels figurent principalement:

Feuilles sessiles ou subsessiles. . . . .   —   *U. pilosa* Hutch.; *U. Gossweileri* Hutch.

Feuilles pétiolées
    Feuilles pubescentes ou poilues au moins sur les nervures à la face inférieure. . . . . *U. sansibarica* Pax; *Van-Houttei* DeWild.; *Brieyi* DeWild.; *Kirkiana* Muell. Arg.; *benguelensis* Muell. Agr.; *togoensis* Pax.
    Feuilles glabres ou presque glabres ou légérement écailleuses. . . . . *U. Staudtii* Pax; *Heudelotii* Baill.; *Pynaerti* DeWild.; *Bossenge* DeWild.; *nitida* Muell. Arg.; *sansibarica, guineensis, Casteelsi* DeWild.; *Laurenti* DeWild.

Pour les documents fructiferes, nous avons pu examiner une partie du matériel de l'Herbier de Kew et des récoltes de M. le Dr. Fries,—nous nous sommes basé sur la forme du pyrène; arrondi, apiculé, ou émarginé—cordé à la base; sur la suture ventrale droite ou presque, sans appendice ou appendiculée. Nous avons de cette manière obtenu le classement:

Pyrénes arrondis ou cunéiformes à la base, non émarginés-cordés. . . . .   *U. sansibarica* Pax.
Pyrénes cordés ou apiculés.
    Suture ventrale droite, légérement en creux ou légérement bombée, à appendice au sommet ou à la base proéminent vers le centre du fruit. . . . . *U. Heudelotii* Baill.; *prominenticarinata* DeWild.; *sapini* DeWild.; *Masuku* DeWild.[4]
    Suture ventrale droite, légérement en creux ou légérement bombée sans appendice. . . . . *U. Gossweileri* Hutch.; *verruculosa, Vermeuleni* DeWild.; *Bossenge* DeWild.; *angolense* Hutch.; *VanHouttei* DeWild.; *nitida* Muell. Arg.; *guineensis* Muell. Arg.; *Kirkiana* Muell. Arg.; *Casteelsi* DeWild.; *Goosensi* DeWild.

Toutes les espèces du genre ne sont pas relevées dans ces deux tableaux, mais ces données suffisent pour faire voir que les deux méthodes de classement amènent à des groupements différents; la concordance n'existe donc pas entre les caractères dont nous nous sommes servi.

Dans de telles conditions il est des plus difficile d'attribuer une valeur à

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[4] Nous insisterons ailleurs sur les autres caractéres des espèces ici signalées, mais non encore décrites.

l'un ou l'autre de ces caractères et par suite de définir par l'un d'eux, avec certitude, des espèces.

Nous serons donc forcé, et pendant probablement longtemps encore, de créer des espèces nouvelles, de valeur peut être bien secondaire.

Ces créations sont absolument nécessaires, car seules elles permettent de mettre en vedette certains organismes dont il faudra soumettre les caractères à de nouvelles recherches approfondies.

Il résulte de ces considérations que toutes les études systématiques si nombreuses, accumulées jusqu'à nos jours, qu'elles soient le résultat de recherches des botanistes anciens, Linné en tête, ou des botanistes modernes, doivent être considérées comme provisoires; et il en sera de même de toutes les autres recherches biologiques!

Nous ne constituons rien de définitif, nos études amènent journellement des faits nouveaux, nous en recherchons l'explication et essayons par la synthèse à nous rapprocher de plus en plus de la vérité, que nous n'atteindrons probablement jamais.

C'est surtout sur cette situation transitoire que nous désirons insister et cela dans tous les domaines, il faut que tous les systématiciens, comme tous les botanistes et tous les scientistes, aient le courage d'admettre que leurs travaux ne sont rien de définitif, et qu'ils doivent être basés sur une connaissance la plus précise possible de l'organisme qu'ils ont mis en expérience, ils doivent être très objectifs.

C'est là, il faut bien le dire, une très grande difficulté surtout quand il s'agit de rechercher, d'après un petit nombre de documents des caractères de parenté. Cette recherche est, faut-il l'ajouter, indiscutablement sous l'influence de notre état d'esprit, elle donnera donc, sans le moindre doute, des résultats pouvant différer plus ou moins sensiblement suivant les moments et plus fortement encore suivant les auteurs.

Si, nous ne pouvons assez le répéter, l'espèce existe dans le monde, et nous en sommes persuadé, il n'est nullement certain que nous arrivions jamais à la définir, à la reconnaître exactement; ce que nous considérons comme espèce, même du type "linnéen," sera toujours une création de notre esprit.

PRINCIPLES AND PROBLEMS OF PLANT NOMENCLATURE[1]

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It is generally agreed that the present condition of plant nomenclature is unsatisfactory. Systematic botanists have to spend much time studying the names of plants which might more profitably be devoted to study of the plants themselves. Taking the classification of Dalla Torre and Harms as a basis, one species out of every eight among the Phanerogams bears different names under the International Rules and American Code. If smaller genera are adopted, the proportion of different names is probably less. In any case, this divergence in nomenclature seriously retards the progress of systematic botany.

As we all desire the advancement of botany, we should all work together to secure closer agreement on nomenclature than exists at present. Agreement as to the *rules* of nomenclature must necessarily be preceded by agreement as to its *object* and *basic principles*. I will attempt to define these.

Object of nomenclature. The object of taxonomic nomenclature is to supply a concise and rapid means of indicating the identity of any taxonomic group, so as to enable botanists and others to make use of the data recorded for the group. This object is purely practical. It has nothing to do with ethics. Unfortunately, a personal element has been introduced into nomenclature by the general practice of citing the "author" responsible for each name, and it has been argued that it is "dishonest" to reject a name proposed by an earlier author in favor of one proposed by a later author. Even supposing that the "credit" to be assigned to a botanist could be measured by the number of new names which he has published, his personal interests should obviously be subordinated, if necessary, to the advancement of the science. The object of nomenclature would be defeated if a very well known name were superseded by an earlier little known name, since the change would make the recorded data less accessible.

Acceptance of this object involves the recognition of three *basic principles*:

I. *Unambiguity of Names.* Each name should be unambiguous.

II. *Definition of Groups.* Each name should be associable with a definition of the group for which it is proposed.

III. *Fixity of Names.* Names should be altered only when absolutely necessary, since alterations make the recorded data less accessible.

I. *Unambiguity of Names.* In order to secure unambiguity it is necessary that:

A. One set of rules should be observed by all botanists.

B. Each name should be restricted to one group, that is, of two or more homonyms only one should be accepted as valid.

C. Each group should bear only one name, that is, of two or more synonyms only one should be accepted as valid.

D. Provision should be made for the possibility of restriction of the limits of each group.

II. *Definition of Groups.* In order to be adequate the definition of a group should be two-fold:

A. A description of its characters should be supplied, for example, in the case of a genus a generic description should be given, in the case of a species a specific description.

B. An indication of the elements of which it is composed should be given. In the case of a genus, the species included in it should be cited. In the case of a species the specimens included in it should be cited.

III. *Fixity of Names.* In an ideal state of nomenclature as long as the limits and position of a group remain unaltered, so long should the name of that group remain unchanged.

METHODS OF CARRYING OUT THE THREE BASIC PRINCIPLES

(1) *Priority of publication.* The most effective method of securing unambiguity and fixity is that of priority of publication. This method is a good servant, but a bad master. For practical reasons it has certain limitations.

(a) *Starting point.* Obviously we cannot go back to Pliny or Dioscorides—much less to earlier writers—for our nomenclature. The publication in 1753 of the first edition of Linné's "Species Plantarum" has been generally accepted as the starting-point for the nomenclature of Phanerogams, since it was in that work that Linné introduced his binary system of nomenclature. The question of a suitable starting point or starting points for the various groups of Cryptogams is one which concerns cryptogamic botanists and should be decided by them.

(b) *Definition.* The priority of a name does not take effect until a definition of the group has been given.

(c) *Provision for exceptions.* Even as limited above, the method of priority of publication would involve the disappearance of many well-established names, unless exceptions are admitted.

(2) *The type-method.* The essence of the type-method is the acceptance of a particular unit or so-called "type" to which each name is permanently attached (whether as an accepted name or as a synonym) however the limits of the group may be altered. The weakness of the type-method is that in many cases there is disagreement as to which unit should be regarded as the type, and in others there is no particular reason for regarding any unit as the type. In order that the type-method may operate in accordance with the basic principles of nomenclature there must be: (a) Agreement as to individual types. (b) Provision for exceptions.

RULES OF NOMENCLATURE

Each rule should be judged in the light of how far it effects the object and conforms to the Basic Principles of Nomenclature. Judged in this manner, both the International Rules and the American Code exhibit certain defects.

(1) *Defects in the International Rules.* (a) The principle defect in the International Rules is that they lead in some cases to ambiguity. This is a result of the provision under which a later homonym may be used if an earlier homonym is universally treated as a synonym. Apart from the difficulty of defining "universal" treatment, taxonomic opinion is constantly changing. Owing to the adoption of smaller genera, a generic name formerly treated as a synonym may come into general use, and a later homonym, which was formerly accepted under the Rules will then have to be rejected.

(b) Another defect in the International Rules is the acceptance of generic names accompanied by a description, but without any indication of the species included in the genus. Any botanist who has tried to fix the application of the numerous generic names proposed by Necker, for example, knows that it is impossible to determine the correct application of many of them with any degree of certainty.

(c) A third defect in the International Rules is the insistence on Latin descriptions of new groups. This has become a dead-letter by force of circumstances. Since 1908 over ten thousand new species of Phanerogams have been published without Latin diagnoses and their names are therefore invalid under the rules. Under the rules it is open to anyone—if he is sufficiently misguided and has enough time to waste—to give a short Latin diagnosis of each species and change all these ten thousand names, which is absolutely contrary to the basic principle of fixity of nomenclature.

(2) *Defects in the American Code.* The principal defect in the American Code is that it ignores the basic principle of fixity of nomenclature. In the name of "consistency" it rejects all exceptions, and so changes hundreds of well-known generic names. Many of these changes have already been made, but it is not generally realized how many generic names still remain to be changed under the provisions of the American Code. Such changes are due to four main causes: (a) adoption of prior synonyms; (b) adoption of prior homonyms; (c) rigid application of the type-method; (d) rejection of generic names unaccompanied by binary specific names.

(a) *Adoption of prior synonyms.* The important tropical genus *Combretum* (Combretaceae) (1758), which includes several hundred species, must now bear the name *Grislea* (1753). But the name *Grislea* has been erroneously applied from 1758 down to the present day to a genus of *Lythraceae*, so that great confusion would be caused by its transference to the genus hitherto known as *Combretum.* Many prior synonyms still remain to be discovered. An expert in the type-method could revive many forgotten names by going systematically through Adanson's "Familles des Plantes."

(b) *Adoption of prior homonyms.* The well known generic name *Calceolaria*

(Scrophulariaceae) is replaced by *Fagelia* under the Code, owing to the existence of the prior homonym *Calceolaria* Fabr. (*Orchidaceae*). Not only botanists but horticulturists and the general public will be inconvenienced by the replacement of the name *Calceolaria* by *Fagelia*.

(c). *Rigid application of the Type-method.* The Linnean generic name *Achyranthes* (Amaranthaceae) has been generally restricted to the genus typified by *Achyranthes aspera*. Standley has recently stated that another species is to be regarded as the type, and has accordingly transferred the name *Achyranthes* to the genus commonly known as *Alternanthera*, also belonging to the Amaranthaceae. This transference of the name is bound to result in confusion.

(d). *Rejection of generic names unaccompanied by binary specific names.* The generic name *Doliocarpus* Rol. (Dilleniaceae) was published in 1756 with a generic description and descriptions of two species, but without binary specific names. Binary names were supplied by Gmelin in 1781, but in the meantime Aublet in 1775 had described the same genus under the name *Soramia* with a binary specific name. Hence *Soramia* should replace *Doliocarpus* under the Code. The bibliographical work in Britton and Wilson's "Flora of Porto Rico and the Virgin Islands" seems to have been very carefully done, but these authors have nevertheless overlooked the fact that *Doliocarpus* should be replaced by *Soramia*. Many similar changes under the Code still remain to be discovered.

THE POSSIBILITY OF A WORLD-WIDE AGREEMENT ON NOMENCLATURE

If botanists can agree as to the object and principles of nomenclature, it should be possible to arrive at agreement as to rules. The following basis for agreement is suggested:

Sect. I. Homonyms.

1. All combinations which are later homonyms are to be rejected.

2. All well-established generic names which are later homonyms are to be conserved. All other generic names which are later homonyms are to be rejected.

Sect. II. Definition of new groups.

3. Latin diagnoses are not to be compulsory, but botanists publishing descriptions of new groups in other languages are to be recommended to supply brief Latin diagnoses for the benefit of their fellow workers.

4. Names of genera are not to be accepted unless they are associated with generic descriptions.

5. Names of genera are not to be accepted unless one or more species included in them are cited. These species need not have binary specific names. Provision is to be made, however, for conserving well established generic names which do not comply with this requirement.

Sec. III. Type-method.

6. The type-method is to be accepted, but provision is to be made for exceptions in cases where its rigid application would involve the rejection of well established generic names.

7. Wherever the type-species of a genus is in dispute, or there is no species

with greater claims than others to be regarded as the type, a standard-species is to be selected by agreement.

Sec. IV. Conserved Names.

8. A list of conserved generic names is to be recognized. These names are to be well established names which would be rejected by the unrestricted operation of the Rules. A statement of the reasons for conserving each name is to be supplied. The preparation of the list is to be entrusted to an International Committee which will consider suggestions for further additions to the list and be responsible for making any additions that may be required from time to time.

Sect. V. Permanent International Committee on Nomenclature.

9. A permanent International Committee on Nomenclature is to be appointed with the following duties:

(a). To interpret the Rules of Nomenclature where their precise effect is doubtful or is in dispute.

(b). To carry out the duties indicated under Sect. IV.

EFFECT OF THE PROPOSED AGREEMENT

The proposed agreement would combine the best features of the International Rules and the American Code. It would get rid of the ambiguity which sometimes results from the International Rules and would at the same time avoid the serious name changes which result from the adoption of the American Code. The proposed rules would be modeled largely on the American Code, but owing to the recognition of a list of conserved names, their practical effect would be to maintain established nomenclature very much as it is at present under the International Rules.

STATEMENTS ON THE SYSTEMATIC STUDY OF VARIABLES[1]

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The speaker at the outset laid down the proposition that the greatest quest or concern in biology is to discover origins. His other statements were in explanation of the preparation for this quest and the means of approach to it. We are yet at the beginnings of the quest. The present account is an abstract and condensation of the statements presented at the Congress.

Precedent to the quest itself is accurate identification and adequate record of the forms of life. We cannot make progress until we are able to speak of the kinds of organisms with exactness. We must both know the forms and systematize our knowledge of them. The importance of these systematic studies is therefore primary and fundamental. The more perplexing and variable the forms, the greater is the necessity for diligent search and research of them.

Our present natural history system is dated from Linnaeus. Its particular purpose is to designate species. To Linnaeus, "We count as many species as there were different forms created in the beginning."

"There are as many species as there were different forms created by the Infinite Being in the beginning; and these forms, according to the laws of their generation have produced more but always like unto themselves. Therefore there are as many species as there are diverse forms or structures occurring today." (Linn. Phil. Bot. no. 157.)

Now, however, two revolutionary concepts are common property: (1) that species have ancestry; (2) that the individuals of the species are not homogeneous, perhaps not even harmonious, among themselves. That is, the Linnaean concept breaks down.

We are under the necessity of nomenclature. For convenience we desire the names to be uniform. But the plants are not invariable. Yet there are those who still hope for a fixed and invariable nomenclature: the statement of the case discloses the futility of such hope.

The effort to petrify nomenclature has resulted in the centering of affection and concern on the invariables, that is, on the "good species." These are the easiest. They go best in a book.

It is the present assumption, in general, that the invariables represent an approximate completion of a phylogeny. Conversely, the variables are assumed to be in active evolution; if so, then they are the most significant for study: this is or should be the contemporaneous point of view.

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 17, 1926. The account here included is essentially an outline of an argument prepared for the Section under this title.

The shift in outlook is well represented by the statement of Asa Gray, 1869, in his "field, forest, and garden botany" in one of the key divisions in Rosa, that "the greater part of the modern garden roses are too much mixed by crossing and changed by variation to be subjects of botanical study." When it became my part, twenty-five years later, to revise the book I omitted the conclusion of the sentence, "to be subjects of botanical study."

In these various ranges we are dealing with the broad subject of SYSTEMATIC BOTANY or BOTANICAL SYSTEMATOLOGY, in which there are four great divisions: (1) *Identification*, or the critical discernment of the kinds; (2) *phytography*, the art of diagnosis and description; (3) *onymy* (orismology) or the science of names; (4) *taxology*, the science of classification of the kinds, including the practically more specialized term taxonomy (which is often at present generalized, as in the title of this Section). Involved in all these divisions in *terminology* (glossology), or a collection of terms.

We approach our anatomy and physiology in a scientific research spirit, at the same time that we are likely to exhibit a high-school attitude toward botanical systematology. Yet a careful critical knowledge of the kinds is a necessary starting-point for any work that employs binomial nomenclature. It is a *conditio sine qua non* for painstaking work in cytology, embryology, genetics, horticulture, ecology, phylogeny, philosophy.

It is a pity that onymy is involved in taxology, for whenever we change our conceptions of genera and species we change the name of the plant. Herein is a fundamental weakness in binomial nomenclature. The consequences of this defect were presumably not foreseen by Linnaeus and his contemporaries inasmuch as origins and phylogeny were not then under consideration.

It is a misfortune that a person cannot exercise his talents freely in the shifting of genera without interfering with the names of plants. We should have gained much in simplicity of literature, in clarity and in popular usage, if we had had a mononymy or other arrangement instead of a taxonomic dionymy.

As long as the names of plants carry taxonomic opinions we cannot hope, of course, for a fixed or even a dependable nomenclature.

In our terminology we are still special-creationists. We yet apply the term *species* to invariables and variables alike. If we attempt to recognize epochs or stages, we make them merely phases of species, as *varieties*, *forms*, and the like.

In the increasing effort to Latin-name every plant we see, we string out the subordinates and we may soon be back to the old ante-Linnaean descriptive phrases. The great need is for terms to designate categories without implication of rank or origin.

If I make my remarks fairly intelligible I must cite cases. Very well: for some years I have been fascinated with *Rubus*, *Brassica*, *Vitis*, *Prunus*, all high variables, and *Rubus* is probably the acme of variables among sporophytes. On the other hand, I am tantalized by the palms which for the most part present an opposite situation. The variables are particularly well expressed in the cultivated flora; and this flora, therefore, will assume peculiar significance, as it

did to Darwin, when we come really to attack the modern question of origins.

I am not here to discuss *Rubus*, but it serves my purpose to use it for the moment as a highly developed illustration of variables. You may substitute *Carya* or *Hicoria*, *Hieracium*, *Aster*, *Eschscholzia*, *Rosa*, *Crataegus*, or what you will. When I mention *Rubus*, it is understood that I have in mind the problem as it appears in North America although I am not without experience in *Rubus* in other countries.

One comes now and then on *Rubus* colonies that belong to nothing. These aberrants have not been studied and, if collected at all, are likely to be put aside as puzzles. They may be species, nascent species, or kinds of nonconformities not yet accounted for in our philosophies. There are four ways of disposing of such plants: (1) Ignore them; this is the easiest way. (2) Throw them loosely or uncritically into some recognized species; this extends the confusion. (3) Assume that they are "hybrids," even though the origin may be wholly unknown or even unindicated; this confuses the confusion. (4) Give them name and diagnosis; this puts them on record; the origin is another question, for a different kind of study.

It will be understood, therefore, that when I write "new species" (or *species nova*), in any of the highly variable groups, I do not use the term in its old formal final sense; I am thinking of a congeries of plants so harmonious within itself and so distinct from all others as to require name and diagnosis if we are to discuss the subject intelligently; and I regret that modern practice has not given us a word of clearer accuracy and significance.

We have kinds of deviations here, perhaps categories of them, that we have not named. I am convinced that we cannot call them *variations* of the usual sort, nor yet *mutations*. If we had the verbal agility of many specialists we should probably have a score of novel words to express our suppositions in the systematic field.

Now it so happens that we have habitually lumped the nondescript deviations amongst the variables under the one term *hybrid*; yet hybridity has also a technical or scientific connotation, to which it should be restricted.

We may well use the old word *species* for the invariables, but with whatever reservations may be necessary, remembering that in Latin it signifies only *that which appears* without implication or assumption of origin or history. For the variables of similar importance, that do not have the metes and bounds, I find myself tentatively using the Latin *classics*, which signifies *a group within a group*. Thereby I escape old connotations and commit myself to nothing except that I have something to describe and record. I shall not even suggest that I may sometime so far forget myself as to write *classis nova* instead of *species nova*; I should have little hesitation in doing so were it not that under present practice it might be taken as an added confusion in taxonomy.

A change of attitude is essential in the approach to these systemic problems both in the details of their consideration and in the appraisal of them in the minds of the profession. On the latter side, there is a common supposition that the systematics have fallen into bad ways if not into actual decadence; this

assumption is unfounded. It is indeed true, in the modern shake-up in systems of nomenclature (much of which was unfortunate and unnecessary), that advantage has been taken of the opportunity to play in names without biological study, but this phase is now largely past and all but the systematists may begin to forget it; it is only an episode in the progress of botanical investigation. Naturally, the work of systematists, as of others, is of unequal integrity and importance, but I venture that never has there been so much thoroughly good systematic work under way and recently published. We are now able, with better and more abundant material and with broader knowledge, to improve and to correct much of the old work. Those who easily say that contemporaneous systematic work as a whole is degenerate are either prejudiced or misinformed. It is worthy of full respect as a major and dignified contribution to the larger biology.

The study of the variables from the point of view of the systematic botanist calls for particular caution in (1) restraint in the treatment, (2) in the estimate of hybridity, (3) in the necessity of better field work, and (4) in the attitude toward phylogenies.

(1) The variables tempt us into unrestraint. The forms are so numerous and their relationships so baffling that we are likely to be led into tempting speculations as to their systematic position from mere superficial resemblances and contrasts. For the most part, we have been unsuccessful in the systematology of the ultra-variables, due in large part to the effort to apply to them the same practice and the same onymy that we are accustomed to follow with the invariables and monotypes. Probably we shall need to recast our categories and to challenge our familiar concepts before we can make marked progress in dealing with them. I am not convinced that the accustomed practices will bring order out of the difficulty; and, in fact, perhaps orderliness as understood by the systematist is not an essential part of the treatment.

(2) Hybrids. The variables lure us into the swamps of hybridity. This is particularly true of *Rubus*, in which it is easy to assume that all the intermediate and tangential forms are hybrids. In fact, it is something like an obsession in *Rubus*, and we are developing cross-word puzzles in the genus. In making these remarks I have in mind some of my opinions of former years, and I have no criticism of the findings of others.

It is strange what a different attitude we take in *Rubus* from that in other variable genera. In our tramp we came on a wild tangle of native grapes and blackberries. My friend began at once to disentangle the species of grapes but he dismissed the blackberries summarily by saying that they were all hybrids. Yet there was no more evidence or presumption of miscegenation in the Rubi than in the Vites.

It is an easy escape from difficulty to call a plant a hybrid. We habitually evade responsibility and the necessity of careful field and laboratory studies and of better diagnoses. Hybridity is not a taxologic or descriptive concept; it is more correctly used by the horticulturists and geneticists.

Philosophically, the assumption of hybridity in any case commits us to

the very limitation that inheres in the Linnaean concept of species,—it even more definitely implies origins. Here we may well consider the objections of Alphonse DeCandolle (Étude sur l'espèce) to the Linnaean concept: He considers it illogical, inapplicable, and altogether unworkable, for "to determine whether a form is specific, it is necessary to go back to its origin, which is impossible. A definition by a character that can never be verified is no definition at all." Of course Linnaeus himself never practiced his definition. Probably no one has practiced it.

Inasmuch as an assumption of species inheres in the supposition of hybridity, it may be well to offer a more workable definition of the species concept. As I published it many years ago in a paper on the "Philosophy of species making" (Botanical Gazette 22: 457. Dec. 1896.) a species is "The unit in classification, designating an assemblage of organisms which, in the judgment of any writer, is so marked and so homogeneous that it can be conveniently spoken of as one thing."

Before we can safely postulate hybridity we must know our species in nature: these species we do not yet know in the American Rubi, nor in many other groups in which free hybridity is easily assumed.

As a practical matter we find that no two people agree on the parentages of supposed hybrid Rubi, so that the opinions have little negotiable value. Our increasingly intimate knowledge of hybridity leads us to doubt the value of surface characters in determining this method of origin. I happen to have forty-six herbarium sheets of *Rubus* representing the progeny of recorded hand-crosses; from only one sheet do I obtain a suggestion as to both parents, and that even doubtfully; and this is what one would expect from the present knowledge of hybridity.

We are to expect hybrids to occur rather infrequently as compared with species and to be relatively few in number or restricted in range, usually a few stray plants that are evidently differentiated. Yet some of the supposed hybrids in Rubi are at least as widespread as major recognized species and exceedingly abundant, sometimes extending over more than 1,000 miles of territory. They also occur where neither of the supposed parents has been found. It is possible, of course, for hybrids to be more widespread than parents, but the presumption is the opposite. If such ubiquitous forms are found by subsequent investigation to be hybrids, the crossing must have taken place perhaps hundreds of years ago, and for taxonomic and record purposes may merit full specific names; at all events they should be designated by a nomen rather than by a hybridity formula. If it is true, as some persons suppose, that the garden strawberry, garden verbena, and many others, are of hybrid origin in spite of the fact that they do not separate into categories of dominants and recessives through a century or more when grown from seeds, then we must be justified in regarding them as we do species, and so treating them in systematic work.

[The speaker cited many examples in Rubi to illustrate the points and also discussed certain other plants, particularly in respect to stature-forms and color variations. He discussed particularly the interesting case of the

common garden *Verbena* which is habitually regarded as a multiple hybrid. These various observations and illustrations need not be detailed here.]

Hybridity is a fact, not an assumption or a means of escape from difficulties. Particularly, it is not an agency to express one's theory of taxonomy.

I am by no means disputing hybridism in *Rubus* or in other groups. Undoubtedly there is spontaneous crossing in *Rubus*, but how far it extends and how it is to be recognized cannot yet be stated. We must first know the undoubted species thoroughly well; we must have more careful and extensive field studies; I trust that in time careful anatomical and cytological study will provide reliable checks. We have not yet gone very far in any of these directions. I am not ready, for example, to accept chromosome characters as criteria of species until these characters have been verified in more than one generation of presumable pure-line descent, and under varying conditions. It may be possible to fall into easy error here as well as in the examination of a few herbarium sheets; that is, we are not yet sure that chromosome character is always a mark of species.

(3) It is exactly in the variables that we need extensive and critical field studies. This means also that we have better records, that is, better herbarium material. In the question of identity, a printed paper is not a record: the only record is the plants themselves. Yet we are to remember that while we must indeed have specimens for record, the specimens must not take precedence over plants.

Most of the herbarium material in the variables is represented by strays and pick-ups. The specimens are likely to be fragmentary and incomplete and to represent such limited and disconnected areas as to have little geographic significance. I have come to the point in Rubi in which I find it unprofitable to attempt to name miscellaneous collections, no matter how well they may be preserved on the sheets. A similar situation obtains in *Vitis* and in certain other variables.

[The best and most critical collecting, particularly important in the variables, can be undertaken only by the student trained in the groups, whereas much of the material in the herbarium is assembled by general collectors without special interest. The speaker cited examples of the great difficulty of identifying variables from sheet collections alone; often the sight of the plant in the field discloses marks of identification that are otherwise overlooked. He also spoke of the great importance of visiting the type stations, from which the original collections were obtained, to get a definite starting-point in the nomenclature. Good field-work continued over a series of years also establishes the range and the continuity of occurrence. Inasmuch as variables appear in many guises or manifestations, careful field work is necessary for the preserving of the records of variation so that none of the important elements is overlooked.]

(4) The study of variables should eventually give us an insight into phylogeny. The phylogeny of a group or a species is of course quite independent of the taxonomic type. Eventually we may typify species from the point of

view of genesis but as yet we have no real phylogenies in the high variables among plants, although we have charts of systematists showing similarities of visible structure. These charts and diagrams are interesting from the point of view of taxonomy but they may not really express genetic relationships; as yet our measure of even supposed relationships is founded on likenesses, but it is at least subject to doubt whether the statement that "like produces like" is an original or fundamental process in nature. Probably we must go far deeper than organography. Long ago I raised this philosophical question and challenged the accepted point of view, but inasmuch as my effort is now forgotten there is no point in raising the issue.

The future will certainly make radical changes in our conception of species and of variability. Because we have passed the crude special-creation stage we are not to assume that we have yet apprehended the actual genesis, even though we know it is evolutionary. The new findings will demand great and probably fundamental changes in nomenclature, but it is yet too early to anticipate these changes, and in our generation we will do best to hold to the traditional binomial system operated on a basis of bibliographic priority of names. A system of nomenclature cannot be changed successfully, and particularly not to an evolutionary program, until there is prevailing agreement among biologists on phylogenies. Those who rail at nomenclature do not contribute to the solution of the perplexities.

In biology the variables are in many ways the most significant objects and they are most in need of careful study. Necessarily we must conform to the standard practices, but not to the extent that conformation obscures the truth in nature. A new approach to the whole subject of variables is now the greatest desideratum in systematic botany.

THE RELATION OF NOMENCLATURE TO TAXONOMY[1]

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The ultimate aim of botanical taxonomy is to determine the genetic relationships of plant groups. Investigations in all branches of human endeavor require, for the most satisfactory progress, the cooperation of those engaged on a given problem. Comparison of results is greatly facilitated by the use of terms in common. Electricians attempt to agree upon terms to represent their various units. Navigators find it necessary to agree upon standards of latitude, longitude, and time. Astronomers agree on terms to fix the position of heavenly bodies. Botanists are concerned with two kinds of terms, those which apply to organs, to physiological processes, and the like, and secondly to the names by which taxonomic groups are designated. The first category is generally known as terminology, the second as nomenclature. At an early period in taxonomic investigations it was realized that an agreement on the names for taxonomic groups was essential. Names of plants must indicate genetic relationships, on the one hand, and, on the other, must identify the taxonomic groups. Nomenclature serves taxonomy best when it is sufficiently flexible to keep pace with the changing ideas of relationships and when it is sufficiently definite to indicate the groups with precision. A given group should be known to all botanists by the same name. When taxonomy dictates a change in the component parts of a group, botanists should agree on the method by which the corresponding change in the name is made.

The genetic relationship of organisms would be determined by their phylogenetic history, but this history can only be inferred from a discontinuous series of data. There are two chief methods by which we may infer relationships: first by establishing facts in the realm of paleontology; second, by establishing facts in the realm of morphology. Paleontology gives us steps in the actual historic development of the lines of descent. Morphology gives us comparable stages in the lines of descent as represented at the present moment. The paleontological records are distressingly incomplete and are never likely to give more than hints as to relations. Morphology, especially the aspect usually known as comparative morphology, is much more promising. The material is available for an indefinitely large accumulation of facts, the results depending on time and the number of workers. As the facts accumulate the inferences concerning genetic history gradually approach certainty.

It is clear that our concept of relationships is undergoing constant change due to the pressure of additional facts. For practical reasons we develop a

[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 17, 1926.

system of classification based upon relationships and use this as a standard until replaced by a system which better represents the facts.

Nomenclature is a system of records by which taxonomic relations are indicated. As Dr. Bailey aptly says, it is "botanical bookeeping." The records must keep up with ascertained facts. Nomenclature must change in harmony with the changes in taxonomic concepts.

We have seen that taxonomy attempts to represent relationships. Let us look for a moment at another aspect of the subject. From the practical standpoint of convenience it has been found necessary to give names to species, genera, and other taxonomic groups. A system of classification is very useful in identifying and comparing these groups. The accumulation of facts referred to above is dependent on the certainty with which species can be compared. If a botanist investigates the comparative morphology of a group of species, his results can be used by his colleagues only in so far as the species concerned can be identified. A mistake in identity may cause great confusion.

I hope the non-taxonomists will not resent it if I emphasize the necessity for giving particular attention to the identification of the plants they are studying. Experience has shown that the average morphologist or physiologist, though conceding this necessity, may accept identification upon hearsay, general consent, unverified labels, and similar evidence insufficient for the taxonomist.

The present day controversies concerning nomenclature deal with the application of generic and specific names. Those non-taxonomists who have given serious consideration to nomenclatural questions admit the necessity for having names and for changing names to keep pace with our advancing knowledge. They sometimes feel some impatience with changes of names which appear to have no definite relation to taxonomy. That is, the changes seem not to be the result of new facts in morphology but to be irresponsible name-juggling. The non-taxonomists' ideas concerning name-juggling are usually exaggerated, but unfortunately have some basis in fact.

I have shown in another place (Amer. Journ. Bot. May, 1926) that changes in names may be due to a variety of causes. Let us examine the causes with especial reference to their bearing on taxonomy. This examination may suggest proposals for altering our codes of nomenclature that shall be for the benefit of taxonomy and may attract the support of the non-taxonomists. The details of codes must be worked out by experts in nomenclature, for only they can foresee the effect of the laws. However, the principles of a code should be such that the non-taxonomist can appreciate and approve in order that the final code may receive the support of all botanists.

In the article mentioned it was shown that changes of names are due to (1) difference in taxonomic opinion, (2) synonyms and homonyms, (3) incorrect identification. Probably most of my hearers have read this article and I will not weary them with a repetition of the supporting statements. I wish to discuss with you these kinds of changes with reference to their bearing on the progress of taxonomy.

1. Changes of names due to taxonomic opinion. It is clear to all that changes

of names are necessary when required by new facts in morphology. However, the same facts are often interpreted differently by different botanists or by the same botanist at different times. The segregation or combination of groups of species to form genera is a question of opinion even when based upon the same set of facts. The older botanists remember *Euphorbia, Oenothera,* and *Polygonum* as concepts which, in many recent floras, are represented by several smaller genera. Every change of this sort, if accepted, requires a readjustment of our ideas, accompanied not infrequently by resentment that we must learn a new set of names. Codes do not deal with changes of this kind. Is it practicable or desirable that we should make any restrictions on such changes? Personally I think it would be unwise to attempt any control, such as code provisions, because nomenclature is here following taxonomy. The taxonomist should be free to develop his system of classification regardless of temporary inconvenience to the users of names. Each botanist's work will be judged on its merits by his successors.

2. Changes of names due to synonyms and homonyms. The International Rules and the Type-basis Code both recognize priority commencing with 1753, so far as flowering plants are concerned. The former makes exceptions to the rule of priority in the case of genera by recognizing a list of conserved names. The rules further restrict the action of priority by conserving generic and specific homonyms where the older name is not in use.

Right here is the chief point of the nomenclatural controversy. Some botanists wish to retain names in common use regardless of priority. Other botanists wish to readjust names on the basis of priority, thinking thus to obtain ultimate stability though at the expense of present inconvenience. Which policy will be for the best interests of taxonomy?

If botanists of the present could agree on a standard list of typified genera, a great mass of nomenclatural difficulty would be at once cleared away. I do not refer here to a list of nomina conservanda but to a list of accepted or valid genera each with its type or standard species. Agreement on a code to regulate subsequent changes, supplemented possibly by a standard list of economic species, would place nomenclature on a stable basis. No action taken now can bind botanists of the future, yet a reasonable adjustment now would certainly have the advantage of position in the future. Most non-taxonomists wish for stability regardless of priority. They would probably accept strict priority if there were definite assurance that stability could thereby be attained, and a change from one system to another could be made at one jump. However, the advocates of the American Code can give no such assurance and the experience of 35 years since the publication of the original American Code has not given these advocates a very strong talking point.

The advocates of the International Rules wished to conserve names in common use and the rules were formulated with this in view. If there were definite assurance that stability could be attained under the rules there would be no important body of objectors.

To me there is nothing sacred in the law of priority. This law does not

prevail, for example, in terminology and linguistics. It was thought that botanists might more readily reach agreement on the basis of priority than upon, say, an arbitrary list.

Under the circumstances what shall we do? We have the International Rules which represent the majority opinion of an international congress. Is it not better to use this agreement as a basis for discussion? There is a large body of taxonomists in America and Great Britain, who are not satisfied with the International Rules as they stand. The Imperial Botanical Conference (London) passed unanimously a series of resolutions for modifying the Rules. These modifications lead in the direction of the Type-basis Code. Many American botanists have advocated the American Code as a protest against the International Rules. However, a large part of the rules are acceptable to all botanists. I believe it is much more practicable to work for a modification of the International Rules than to continue an attempt to replace them. The general trend of botanical opinion is toward modification of those rules in the direction of the Type-basis Code. But there are features of the latter code which are objectionable to the followers of the Rules. While they are gradually accepting the type concept and certain rules governing the changing of names, which have demonstrated their value, they object strenuously to giving up the list of conserved generic names.

I am, therefore, putting before you the proposition that we unite in an effort to modify the International Rules through legal channels. To be successful this effort will require, first, concessions from the supporters of the International Rules in so far as they will in good faith reopen the rules to discussion, especially along the lines of the British proposals, and second, concessions from the supporters of the Type-basis Code, especially in accepting a list of conserved genera. If a reasonable agreement can be reached, it is probable that the opponents of the Rules will be reduced to a negligible number.

The present Congress can not legislate but it can express its opinion and can adopt resolutions for presentation at the next Congress. Personally I am in favor of (a) adopting the resolutions passed by the Imperial Conference, and (b) appointing an international committee that shall report to the next International Congress.

At this point I wish to interpolate a question. Is it desirable to have a short list of conserved specific names? I have in mind particularly the names of common economic plants. For example, the cultivated wheat is commonly known as *Triticum vulgare*. Yet the earliest name is *Triticum aestivum* L., which, according to the provisions of the International Rules as well as the American Code, is the valid name. Many people besides botanists are interested in the botanical name of wheat and much inconvenience would be avoided by accepting the later name, *Triticum vulgare*. It is doubtful if the earlier name could be forced on a resistant public. May it not be better to conserve *Triticum vulgare*?

3. Changes of names due to misapplication or to incorrect identification. In the recent article referred to I have dealt briefly with this cause of name changes. If the original application of a name has been changed by subsequent

authors, either intentionally or through error, the name, on general principles, should be restored to its original meaning.

REVIEW

Nomenclature does not stand alone. Taxonomy is the classification of organisms; nomenclature is a method of expressing the classification. Nomenclature, then, is a tool for taxonomy. Taxonomy is to other branches of botany what the dictionary is to literature; it enables people to use names in the same sense. Nomenclatural rules and regulations should be judged by their effect on taxonomy. We should avoid a rigid formula or theory in drafting our codes, remembering that we are dealing with living things and a developing science. The original American Code was the logical development of a theory based on priority. If universally adopted, it no doubt, would have given taxonomy a nomenclature as stable as is possible, so soon as the rules could be applied. The application of the rules to all taxonomic groups would take years even when approved by all. As it is, the changes advocated by the American Code have been resisted, though many of its advantages have been conceded as they are better understood. It is clear that our codes of nomenclature must go through a process of evolution in which certain regulations will survive and others will be discarded. Nomenclature can not force itself on taxonomy but taxonomy will gradually adopt so much of a code as has proved its worth. "Taxonomy is primarily a systematic way of stating the known facts of comparative anatomy." Its importance to other (and at present more popular) branches of botany should not be obscured by controversies over nomenclature.

The section on taxonomy will discuss nomenclature at a series of round-table meetings. As a basis for this discussion I submit the following resolutions.

1. That the International Rules be modified to include the proposals adopted at the British Imperial Botanical Conference.

2. That authors in revising taxonomic groups indicate the type species or the standard species of genera, and the type specimens of species when such can be determined.

3. That the application of names in the revised list of Nomina Conservanda be indicated by the type species or the standard species of each genus.

4. That type species and standard species be defined.

5. That the Ithaca Congress appoint an International Interim Committee on Nomenclature. This committee shall consider resolutions referred to it by this Congress and may consider other matters originating with the Committee. Recommendations receiving the approval of the Interim Committee shall be submitted for action to the succeeding Congress.

A FINAL SUGGESTION

After 40 years experience with botanical nomenclature, in which for the most part I have been a consistent advocate of the American Code and later of the Type-basis Code, I am of the opinion that we should approach the matter from a new angle. I am ready to concede that general usage, when this can

determined with reasonable definiteness, should form the basis of our code. The International Rules attempted to formulate rules that would crystallize usage but were not sufficiently precise to accomplish the purpose. Experience has shown that the chief preventable confusion in nomenclature has been due to diverse opinions on the application of generic names. I propose for consideration the suggestion that we create the machinery for establishing a standard list of accepted generic names, each with the species that shall direct its application (type species, or standard species, if you wish). It is not intended to restrict taxonomic opinion but gradually to build up a list of genera which shall be a standard . For example, *Panicum* L.—*P. miliaceum* L. *Echinochloa* Beauv.— *E. crusgalli* (L.) Beauv. Some authors perfer to include *Echinochloa* in *Panicum* but if the group containing *P. crusgalli* is considered a distinct genus it must be called *Echinochloa* regardless of earlier synonyms or homonyms. Such a standard list would include conserved generic names but would be gradually extended to include also all generic names in use. Many details will occur to my hearers, such as the determination of general usage, the method of establishing the machinery (presumably an international committee), and the restrictions as to priority. If the idea is sympathetically received the details can be arranged.

THE FLOATING APPARATUS IN THE FRUIT OF SOME AQUATIC OR LITTORAL UMBELLIFERAE AND THE PROBLEM OF ADAPTATION[1]

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I

Of all botanists, taxonomists, perhaps, have the opportunity of accumulating the most extensive knowledge of the structural behavior of plants, for their studies oblige them to follow, species after species, the morphological modifications in complete systematic series. If it cannot reasonably be asked of them to pursue original research in each interesting case with which they meet, they ought at least to consider it a duty to point out these interesting cases, in order to permit of their being studied by others who are specialized in anatomy and ecology, or who are in positions permitting experimental research. Instead of turning in a circle of relatively few objects, the study of morphological, histological, and ecological phenomena would be usefully renewed by its extension to more varied types.

It was in that spirit that I related in 1899, after a revision of the genus *Oenanthe* for Burnat's[2] Flora of the maritime Alps—which gave me occasion to study the carpology of that group of aquatic Umbelliferae—the very curious facts concerning the floating apparatus in the fruits[3] of species of this genus.

The existence of a floating apparatus in the fruits of some Umbelliferae had been discovered some years before by E. Kølpin Ravn,[4] but the paper of this Danish author seems to have escaped the attention of later botanists just as it escaped my attention in 1899, and the records he gives of the anatomical facts are very summary, partly incomplete. Since that time, I have made several other contributions to the carpology of Umbelliferae, and in various other genera of the family I have met with facts analogous to those encountered in *Oenanthe*. I wish now to summarize our knowledge about the floating apparatus in the fruit of Umbelliferae. It is by no means intended to give here a comparative carpology of all these plants. This would be an interesting, but strenuous undertaking. Some selected examples will be sufficient to characterize

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 18, 1926.

[2] Burnat, E. Flore des Alpes maritimes 4: (cf. pp. 164–176) Geneva, 1906.

[3] Briquet, J. Recherches antomiques et biologiques sur le fruit du genre Oenanthe. Bull Herb-Boissier, ser. 7: (cf. pp. 467–488.); Bull. Lab. Bot. gén Univ. Genève 3: 9–30. *11 figs.* 1899.

[4] Ravn, F. Kølpin. Sur la faculté de flotter chez les graines de nos plantes aquatiques et maré. cageuses. Journal de Botanique publ. par la soc. bot. de Copenhague 19: 143–188. *26 figs.* 1894–95.

the general carpological features and to point out briefly how these features touch upon some of the fundamental problems of biology.

I would say at the outset that all Umbelliferae with variously winged fruits have been excluded. The presence of wings on a mericarp is aways the sign that the dispersal of the fruit is realized more or less with the help of wind. Now the presence of aeriferous parenchyma with pitted walls is very frequent in carpic wings, for many reasons.[5] The result is that winged mericarps of many aquatic or subaquatic Umbelliferae although organized in conformity with a transport by means of wind, can, if they fall in water, float a certain time. One could say emphatically that in this case a flier becomes a sailor without any special education! But this kind of floating is only casual and the function is secondary. Our subject is limited to those aquatic or littoral Umbelliferae whose fruits have no other ordinary means of dispersal than a floating apparatus included in the body of the mericarp, enabling it to travel more or less far, during a more or less long time, on the surface of the water, before landing or sinking, and, if the circumstances are favorable, germinating. The tissue which enables the mericarps to do this has been called "Schwimmgewebe" by Schimper[6] and Haberlandt[7] and as this expression is hardly to be directly translated into several other languages, I have been led to propose for it the general term *pleen-chyma*.[8] Pleenchyma is normally composed in Umbeliferae of masses of cells variously grouped in the mesocarp, forming as many floats or making in the mesocarp a continuous and closed sheath enveloping the inner parts of the pericarp, the endosperm, and the embryo. General characters of pleenchyma are the great lightness of the cells, owing to the relative thinness of their hyaline walls, which are often more or less pitted; the cell walls are finally always lignified and rendered very impermeable to water and air by the presence, possibly, of various substances *ad hoc*, which makes them far more resistant than ordinary parenchymas to the action of cold dilute acid. When the fruits are mature, the cells of the pleenchyma are dead and filled with air which can be expelled only with difficulty. The individuality of pleenchyma is so great that in several instances it owes its full development to the activity of a special meristem. Of course, the tissue called pleenchyma in the fruit of Umbelliferae had not escaped the notice of morphologists and anatomists who have mentioned its existence in special instances, where it forms large floats or thick sheaths; but it had never been closely studied, and its functions were so unknown that with the exception of Kølpin Ravn the qualificatives by which it was designated generally involved errors. Thus certain authors speak of a "spongy tissue," whereas the characteristic of a sponge is to take up water and not to hold air. More-

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[5] Briquet, J. Carpologie comparée de l'Archangelica officinalis Hoffm. et du Peucedanum palustre (L.) Moench. Candollea 1: (cf. pp. 501–520 esp. 518, 519). 1923.

[6] Schimper, W. Die indo-malayische Strandflora. Botanische Mitt. aus den Tropen. 3: (cf. pp. 163 et seq.) Jena, 1891.

[7] Haberlandt, G. Physiologische Pflanzenanatomie. 4th Ed. (cf. p. 499.) 1909.

[8] Briquet, J. Thorella, ombellifère monotype du sud-ouest de la France. Ann. Cons. et Jard. Bot. Genève 17: 235–277 (esp. p. 271). 1914.

over, the term "spongy" evokes the idea of a form and disposition of the cells analogous to that in the spongy chlorenchyma in leaves, which is not at all the case. Others called the tissue "corky," but the cell walls are never suberized. Kølpin Ravn, and formerly I also, had designated pleenchyma by the term "aeriferous tissue,"[9] but this is quite insufficient and has been the cause of the use by subsequent authors of the word "aerenchyma." This translation is also conducive to errors because aerenchyma is a quite different tissue, special to subterranean axes of aquatic plants, homologous to a periderm, and fulfilling other functions.[10] The preceding general indications will be sufficient as an introduction to the description of some selected special cases as follows:

II

HYDROCOTYLE VULGARIS L. (Fig. 1)

The fruit of *Hydrocotyle* is strongly laterally compressed. The mericarps have 5 ribs: a well developed dorsal one, pentagonal-ovate in cross sections; 2 lateral weak ones; and 2 commissural ones, more or less triangular, so that pairs of commissural ribs corresponding to the 2 mericarps apply exactly against each other. The coelum of the mericarp is vaguely rhomboidal.

The epicarp consists of a layer of tangentially stretched elements, the external cell walls thicker than the others, with a thin cuticle, interrupted here and there by stomata situated in the external plane of the epicarpic cells. The mesocarp comprises an exterior leptocarp, and an interior sclerocarp. The sclerocarp is continuous and very tough. This is owing to the fact that on the flanks of the coelum it is built up of 2 inner layers of "prostrate" stereids leaning against 2 or 3 layers of "erect" stereids. At the commissural and at the dorsal ridges of the coelum, the erect stereids predominate entirely. Drude[11] has interpreted the sclerocarp of the mericarps in *Hydrocotyle* as an endocarp, which several other authors had done before him, especially Rompel[12] but this is a disused terminology, which can only produce confusion. It is better to reserve the term endocarp for the inner epidermis of the pericarp.[13] Now the sclerocarp in *Hydrocotyle* is of mesocarpic origin. In mature fruits of this plant, no endocarp, in the above sense, is to be seen; the early disappearance of that tissue is probably owing to the same phenomenon which I have described recently in the genus *Heracleum*.[14] The leptocarp comprises three distinct regions. First, layers of

[9] Briquet, J. "Oenanthe" 1899 l. c. (cf. p. 470).

[10] Schenck, H. Ueber das Aerenchym, ein dem Kork homologes Gewebe bei Sumppflanzen. Pringsheim's Jahrb. für wiss. Botanik **20**: 526–574. *Pls. 23–28*. 1886.

[11] Drude, O. (In Engler und Prantl) Die natürlichen Pflanzenfamilien **8**: (cf. p. 102). 1897.

[12] Rompel, Jos. Krystalle von Calciumoxalat in der Fruchtwand der Umbelliferen und ihre Verwerthung für die Systematik. Sitzungsber. der k. Akad. der Wiss. in Wien. Math.-naturw. Cl. **104**, Abt 1: (cf. p. 427). 1895.

[13] For the terminology of regions in the pericarp of Umbelliferae see: Briquet, J. Monographie des Buplèvres des Alpes Maritimes; p. 26–37, Genève, 1897; Briquet, J. Heracleum, 1924 (see next reference).

[14] Briquet, J. L'anatomie du fruit et le comportement des bandelettes dans le genre Heracleum. Candollea **2**: 1–9 (cf. esp. p. 8, 9). 1924.

microcytic chlorenchyma directly under the epicarp; this is the region of location of the secretory receptacles, imbedded in variable number and of variable caliber, from one extremity of the mericarp to the other. These secretory receptacles possess a regular epithelium and only differ from ordinary vittae by their shortness. Under the chlorenchymatous layers is the pleenchyma. This tissue is here rather macrocytic, consisting of polyhedral, crowded elements, which at maturity are filled with air. The cell walls are thin, finely pitted, lignified, and notably more resistant to the action of cold dilute acids than the
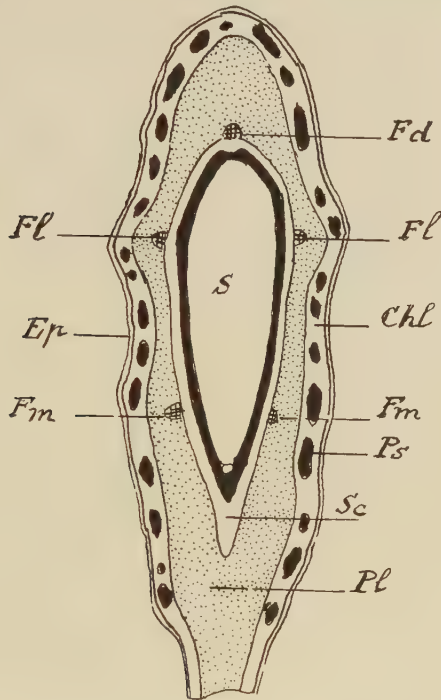
Fig. 1. *Hydrocotyle vulgaris*. Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma with secretory receptacles, *Ps*; *Pl*, pleenchyma; *Fd*, dorsal vascular bundle; *Fl*, lateral vascular bundles; *Fm*, marginal bundles; *Sc*, sclerocarp; *S*, seed.

other parenchymas of the mericarp. Although the cells are crowded, still there are everywhere weak angular intercellular spaces. In the inner layer, the cells contain a big crystal of calcium oxalate. Moreover, such crystals are to be found elsewhere in the neighboring pleenchyma, but far less abundantly and more irregularly. The abundance of pleenchyma varies greatly in the different parts of the leptocarp; it fills the voluminous dorsal rib to a great extent, is weakly developed in the lateral ribs, and fills entirely the marginal ribs; in the vallecules it forms only a thin clothing.

The vascular bundles are extremely reduced; they lean against the sclerocarp in the innermost part of the ribs. The pleenchyma is very difficult to moisten

with cold water; it long withstands boiling; and as the plant lives in marshes and along lakes, floating is in nature a regular process, the mericarp lying on one of its flanks. In fact, there is a single float forming a sheath around the sclerocarp, but this float is considerably enlarged towards its extremities.

Drude has been very unfortunate with the carpology of *Hydrocotyle vulgaris*, for the foregoing notes show that both the description and the figure which this otherwise excellent author has given are wholly wrong in many points.[15] Drude does not figure at all the secretory receptacles, which are easily visible outwardly with the lens, and impossible to miss in any cross section. The author speaks of the existence of big secretory cells in the hypodermic parenchyma, and in contradiction with that, mentions in the diagnosis the occasional presence of "microscopically small" vittae. In fact, the receptacles, as described above, have a regular epithelium whose cells never contain any secretory product, as is also the case in all other Umbelliferae. The whole characteristic of Hydrocotylinae, as given by Drude, will have to be changed. Another important point is this: Drude says that the vascular bundles in *Hydrocotyle* are extraordinarily big and almost entirely fill up the ribs. The contrary is true. The bundles are very small, reduced to some tracheae and one or two sieve tubes. Drude does not seem to have seen them. What the author took for a much developed xylem is pleenchyma, which never bears phloem on its exterior surface. Unfortunately these wrong indications have already been taken up by several later writers.[16]

CENTELLA ASIATICA (L.) URB. (Fig. 2)

In this species, the fruit is also strongly laterally compressed. The equatorial cross section has the form of an ellipse truncated at the commissure. There are no regularly differentiated ribs. In return, the nerves are more or less connected by anastomoses, and the whole system is outwardly salient, so that in cross section the margin appears festooned, with 5-8 festoons on each side of the mericarp. The coelum of the mericarp is elongate-elliptical in cross section, and the seed (later on the endosperm) fills it entirely; the thickness of the pericarp is everywhere almost the same.

The epicarp consists of tabular regular elements, with rather thick exterior cell walls covered with a strongly folded cuticle, and interrupted here and there by stomata located in the same plane as the neighboring epicarpic cells.

The very thick mesocarp comprises as in the preceding species an external leptocarp and an internal sclerocarp. The outer layers of the leptocarp consist of microcytic chlorenchyma, surrounding a very thick zone of pleenchyma.

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[15] Drude, O. (in Engler und Prantl), op. cit. p. 102, 103, 104. Fig. 43A and 44.

[16] The wrong indications relating to the secretory system have been partly corrected: cf. Styger, Jos. Beiträge zur Anatomie der Umbelliferenfrüchte. (cf. p. 9), Zürich, 1919. And before the preceding (Reichenbach, H. G. fil. Icones florae germanicae et helvaticae **21**: (cf. p. 1.) 1867), the facts had been correctly stated as follows: "Tota epidermis sicca rufoverrucosa ob conceptacula oleifera supposita." Calestani, Contributo alla sistematica delle Ombrellifore d'Europa. Webbia **1**: cf. p. 118. 1905. Also, in the preceding reference the author has briefly but exactly described the mesocarp as "vesiculis oleoresiniferis irregulariter dispositis praeditum."

The cells of this pleenchyma are relatively macrocytic and have a tendency to become stretched radially. The cell walls are thin, lignified, delicately pitted and remarkably resistant to the admission of water. The intercellular spaces are much reduced and localized on the angles of the cells. The innermost layer of the pleenchyma contains large crystals of calcium oxalate. The very thick sclerocarp is composed on the flanks of several layers of prostrate stereids, while at the commissural and dorsal extremities, it forms a swelling of (erect) stereids. From these two extremities depart two stereic plates which
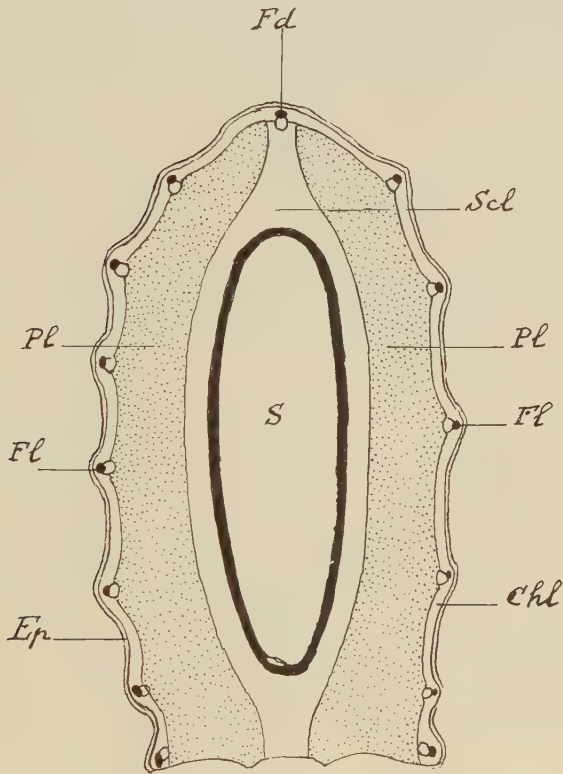
Fig. 2. *Centella asiatica.* Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Pl*, pleenchyma; *Fd*, dorsal and *Fl*, lateral vascular bundles, each with an intrajugal exterior secretory canal; *Scl*, sclerocarp; *S*, seed.

traverse the whole leptocarp and join, one of them the top of the dorsal rib, the other the commissure; these two plates consist of (erect) stereids. In that manner, the pleenchyma is completely separated into two long floats parallel to each other and perpendicular to the commissural plane of the fruit.

The vascular bundles, located in the salients of the nerves and nervules, are about circular in cross section; they are imbedded in the chlorenchyma layers of the leptocarp. Each bundle is accompanied by a small vitta, lying outside the phloem in the plane of symmetry of the bundle, or also laterally

situated. There are as many vittae belonging to anastomoses as nervules affected by the section.

The endocarp is composed of a layer of cuboidal, very regular elements, with somewhat suberized cell walls. The endocarp detaches itself easily from the sclerocarp and remains often fastened to the crushed remains of the nucellus and of the raphe.

Centella asiatica seems sometimes to live at the borders of moist forests, but is specially abundant in marshes, along lakes and rivers. The floating of the fruit is accomplished as in *Hydorcotyle vulgaris*.

I would add to these notes the following observation: When Urban gave a renewed definition of the genus *Centella*, accompanied by a figure representing the cross section of a mericarp[17], he said nothing about the vascular bundles and their vittae, nor about the tissues of the leptocarp (chlorenchyma and pleenchyma). The consequence has been that Drude must have considered the absence of vittae as a confirmation of this negative character attributed by him to Hydrocotylinae. But *Centella asiatica has vittae*, entirely homologous to the intrajugal vittae of other *Umbelliferae*. The exact carpology of all Hydrocotylinae is still to be investigated and will be a necessary preliminary step in any taxonomic revision of that phylogenetically very interesting and important group of Umbelliferae.

CICUTA VIROSA L. (Fig. 3)

The mericarps of this species are approximatively isodiametrical in cross-sections of the equatorial region, but they are made dissymmetric by the inequality of the 5 floats.

The epicarp consists of rather narrow tabular cells, with moderately thickened exterior cell walls, covered with a folded cuticle; the stomata are relatively big and situated at the external level of the epicarp.

The epicarp is subtended under its whole surface by a thin clothing of microcytic chlorenchyma. More deeply, the place of the chlorenchyma is taken by a macrocytic parenchyma, whose elements are generally at maturity strongly crushed. There are 6 extrajugal vittae, of which 4 are vallecular and 2 commissural, these last ones standing very near each other. These vittae are voluminous, abundantly diaphragmed, circular in section at first, often somewhat tangentially stretched later on. Of the 5 roundish and not very salient ribs, the dorsal and lateral ones are the weaker; the marginal ribs are more strongly developed. All of them bear emergences, in which the mesocarpic chlorenchyma penetrates. It is on the histological structure of these ribs that the interest of the carpology of *Cicuta* is concentrated. Each rib is almost entirely occupied by a large float. At the internal limit of the float a very small vascular bundle is situated. In young mericarps, the bundle leans externally against a rather macrocytic parenchyma containing 1–4 small intrajugal vittae. This parenchyma develops gradually in pleenchyma. To this

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[17] Urban, I. (In Martius) Flora brasiliensis **11**(1): cf. p. 286, tab. 78, I. fig. 12. 1879.

end, its cells divide actively, at first in various directions, producing later on especially tangential new walls. This kind of meristem pushes the intrajugal vittae towards the periphery and crushes them. In mature fruits, there is mostly nothing more of them to be seen, unless the tissue be submitted to a careful treatment with chloral hydrate. At last, the pleenchyma crushes completely the primitive parenchyma in which it has been developed, as well towards the periphery as towards the coelum. The cells of the pleenchyma are mostly voluminous, with thin, lignified walls, the ones resulting from the last divisions remaining very delicate. All are very impermeable to water, without pits or with rare and very minute pits. The intercellular spaces are mainly located at the angles of the cells.
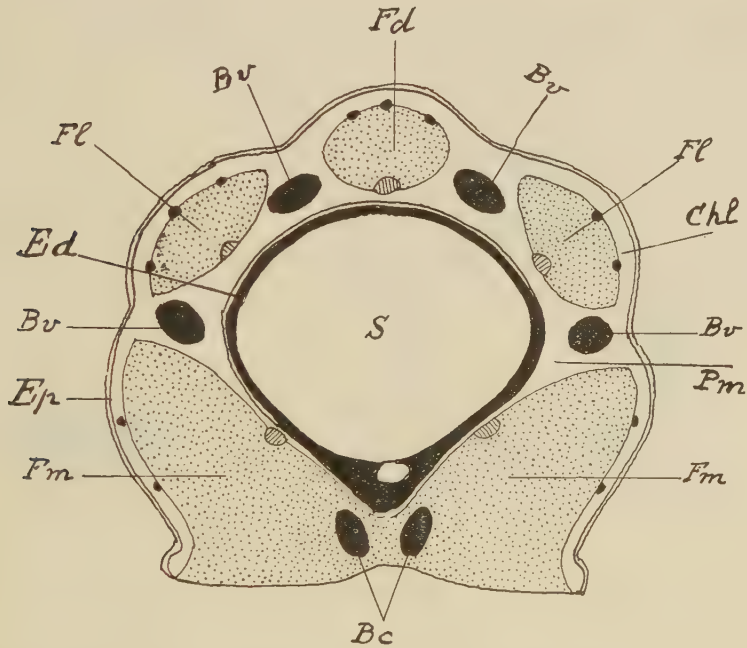
Fig. 3. *Cicuta virosa.* Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Pm*, macrocytic parenchyma; *Fd*, dorsal, *Fl*, lateral, and *Fm*, marginal floats each with a vascular bundle on the inner side and several secretory canals on the outer sides; *Bv*, vallecular vittae; *Bc*, commissural vittae; *Ed*, endocarp; *S*, seed.

The endocarp, generally much crushed in mature fruits, consists of tabular cells without particular properties.

In spite of their somewhat awkwardly heavy appearance, the mericarps float easily, generally with the commissural surface upwards, because of the presence on that side of the larger floats. *Cicuta virosa* is found along deep and very watery marshes and lakes.

BERULA ANGUSTIFOLIA KOCH (Fig. 4, 5)

(*Sium angustifolium* L.)

The fruit of *Berula* with 2 vaguely pentagonous mericarps in cross-sections, presents very interesting pecularities.

The epicarp consists of rather voluminous, tabular, outwardly convex cells, with strongly thickened exterior cell walls and a folded cuticle; it is interrupted here and there by small stomata situated in recesses of the epicarp.

The mesocarp is entirely leptocarpic and comprises two very highly differentiated regions. The exterior, less developed region, is occupied by chlorenchyma, of which 1–2 outer layers are microcytic, while the inner ones are macrocytic, less rich in chloroplasts, very loose, with enormous aeriferous intercellular spaces. Imbedded in the chlorenchyma and located in each rib is a small vascular bundle, more or less circular in cross section, accompanied
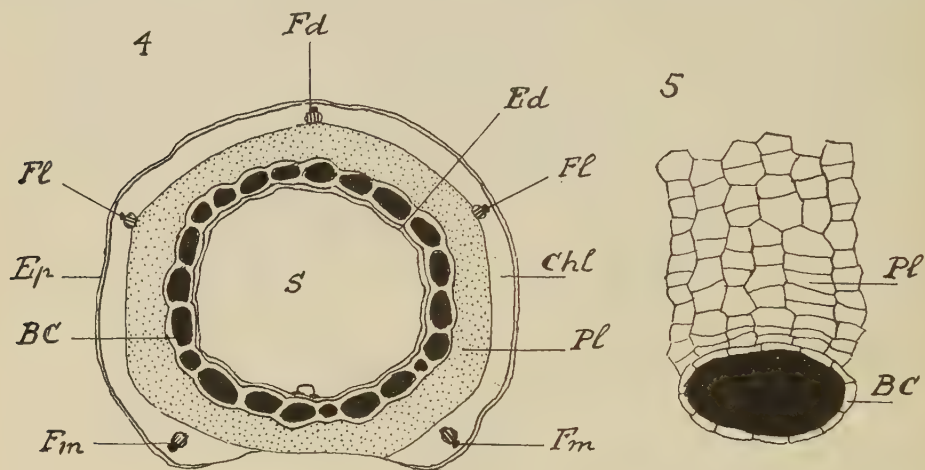
Fig. 4. *Berula angustifolia.* Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Fd* dorsal, *Fl* lateral and *Fm*, marginal vascular bundles, each with externally situated secretory canal; *Pl*, pleenchyma; *Bc*, belt of cyclic internal vittae; *Ed*, endocarp; *S*, seed.

Fig. 5. *Berula angustifolia.* Magnified cross section of the pleenchyma; *Pl*, showing the radial disposition of cells owing to repeated tangential divisions; *Bc*, internal vitta with its epithelial sheath.

outwardly by an intrajugal vitta. The interior region of the leptocarp consists entirely of pleenchyma which forms a continuous and thick sheath, enveloping from all sides the deep regions of the mericarp. In young mericarps the layers are few, but they rapidly grow in number by successive tangential (7–10) divisions. In that manner, regular series of radially, more or less regularly, disposed elements are obtained, resembling the regular, radial series of cells in a phellogen. However, these cells have none of the characters of cork: they lose at last, it is true, their protoplasts and become filled with air, but the cell walls become lignified, never suberized, not readily permeable to water, although they are often more or less pitted. Inwardly, the pleenchyma borders

directly on the voluminous vittae in cyclic disposition (generally 15 to 22). The epithelia of the vittae are at maturity most often in lateral direct contact with each other. The vittae present in longitudinal sections 7–12 splendidly developed diaphragms; their summit is club-rounded, while the base is tapering. The endocarp consists of small cuboidal cells without remarkable peculiarities.

Berula angustifolia is an inhabitant of waters, in pools, marshes, and along lakes; it is also frequently found growing in running water. The mericarps float very easily, rolling like kegs, owing to the highly symmetrical disposition of all the tissues and particularly of the pleenchyma.

It must be noted that Reichenbach[18] has described the pericarp of *Berula* as "suberosum fasciculis ligneis obliteratis (semper?)". The expression "suberosum" applied to the pericarp seems to indicate that he sought the bundles in the pleenchyma, where they are not. Calestani[19] has gone farther and says the pericarp has no vascular bundles at all. If that were true, *Berula* would differ in this respect from all known Umbelliferae. But it is not the case.

CRITHMUM MARITIMUM L. (Fig. 6)

I resume here the paper which I devoted 3 years ago to the fruit of this highly interesting species[20].

The mericarps are pentagonal in equatorial cross-sections, dorsally compressed, so that the commissural side is twice broader, and often even more, than the dorsal vallecules, and these are broader than the lateral vallecules.
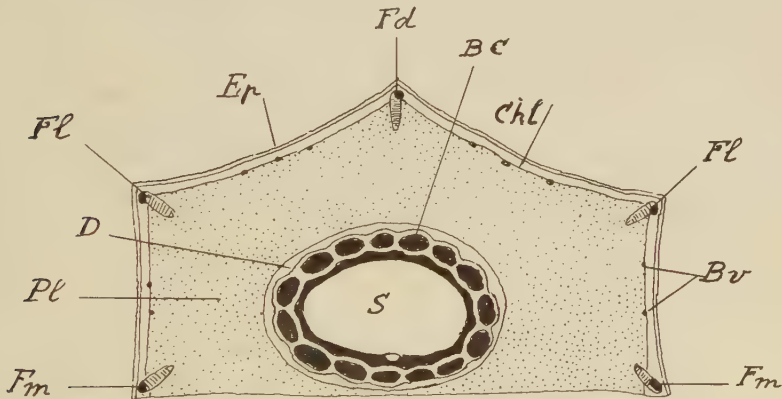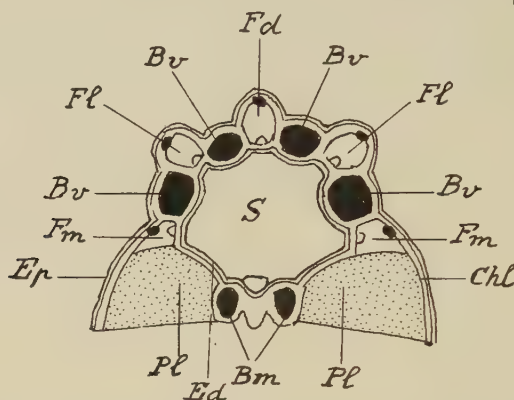

Fig. 6. *Crithmum maritimum*. Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Fd*, dorsal, *Fl*, lateral, *Fm*, marginal vascular bundles each with an externally situated secretory canal; *Pl*, pleenchyma with obliterated minute vallecular external vittae, *Bv*, *D*, layer of desaggregation; *Bc*, belt of cyclic internal vittae; *S*, seed.

[18] Reichenbach, H. G. (fis) Icones florae germanicae et helveticae 21: (cf. p. 14). 1867.
[19] Calestani, V. Contributo alla sistematica delle Ombellifère d'Europa. Webbia 50: (cf. p. 138). 1903.
[20] Briquet, J. Carpologie du Crithmum maritimum. Compt. Rendu Soc. phys. et hist. nat., Geneva, 40: 115–121. 1923.

The vallecules are slightly concave while the commissural face is plane except in its middle. The tissues constituting the wholly leptocarpic pericarp are the epicarp, the hypodermal chlorenchyma, the pleenchyma, the disjunction layer, the deep parenchyma, the endocarp. Moreover, we have the vascular bundles accompanied by intrajugal vittae, vallecular external vittae (very rarely to be seen in ripe mericarps) and lastly the deeply situated strongly developed cyclic vittae.

The epicarp consists of tabular cells, with thickened exterior cell walls covered by a strongly folded cuticle, interrupted here and there by rare stomata.

The hypodermal chlorenchyma is constituted by 3-4 layers of elements similar in size to those of the epicarp. At first, the intercellular aeriferous spaces are abundant in the chlorenchyma and the stomata command deep respiration chambers. In mature mericarps the hypodermal chlorenchyma is quite crushed, so as to make a thick cushion; the stomata lose their function and the communications between the pleenchyma and the exterior are rendered difficult. This is a frequent process of isolation for pleenchyma in mature mericarps of Umbelliferae.

The pleenchyma occupies by far the greatest part of the pericarp. Its large cells have very thin, hyaline, lignified walls. In many cases, the cell walls are quite smooth; however, here and there, some rare and small, roundish or elliptical, irregularly distributed pits can be seen. There is no trace of suberization. Nevertheless, doubtless as a consequence of the presence of some insulating substance in the cells walls, the walls are resistant to the action of cold dilute acids and very impermeable to water and air. In the neighborhood of the sinus of insertion of the carpophore, the cells of the pleenchyma are smaller, more crowded, with thicker more strongly lignified walls. As concerns the origin of the enormous sheath of pleenchyma in the mericarps of *Crithmum*, it must be noted that it arises in the 2–3 middle layers of the younger mesocarp. The cells of these layers are early recognizable by their rarer chloroplasts. These disappear while the cells divide actively in all senses. The result of this work of division is the formation of a thick coating in which nothing of the regular radial disposition realized in *Berula* is to be seen, the protoplasts die and the cells become filled with air.

The pleenchyma is limited inwardly by a layer of large cells, whose walls are of pure cellulose and thin to the end. It is the *layer of disjunction* in which the radial cell walls become torn at maturity, so that the whole of the inner parts of the mericarp become separated from the outer ones just described. The ecological signification of this very rare phenomenon is still obscure[21].

The deep parenchyma comprises 2–3 layers of cells strongly stretched tangentially; they are radially so crushed as to become utterly unrecognizable at maturity. The same case presents itself for the endocarp, which constitutes a thin clothing all around the coelum of the mesocarp.

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[21] On this question and on the mechanism of disaggregation see: Briquet, J. Carpologie comparée de l' Archangelica officinalis Hoffm. et du Peucedanum palustre (L.) Moench. Candollea **1**: (p. 506, 507, fig. 3). 1923.

The vascular bundles have in cross-sections the form of an ellipse stretched along the bissectrice of the ribs containing the bundles. The vascular plate thus effected penetrates on one side into the pleenchyma, while the other extremity is imbedded in the hypodermal chlorenchyma. The endoxyl of the xylem lengthens inwardly and becomes the center of convergence of the neighboring cells of the pleenchyma stretched in the direction of the bundle. On the other side, the phloem constitutes a narrow beach against which a few pericyclic stereids often lean, or is separated from the chlorenchyma by a simple layer of hyaline parenchyma. The intrajugal vittae are very small and often somewhat crushed at maturity. They stand isolated in the chlorenchyma, either outside of the phloem or frequently more or less laterally to it.

The deeply situated vittae form a continuous circle in the innermost parenchyma of the mesocarp. Their size is rather variable; their number is 16–20 in the equatorial region of the fruit. Roundish, later on elliptical in cross-section, they are salient on both sides, producing an undulating effect on both endocarp and seed. These vittae are regularly provided with diaphragms and somewhat contracted at the level of these, which stand at unequal distances.

The existence of a layer of disjunction outside of the cyclic vittae has caused Reichenbach fil. to regard the vittae as standing inside of the endocarp.[22] This wrong interpretation has been unfortunately reproduced by Drude.[23]

In my paper on the carpology of *Crithmum*, I failed to detect the small exterior vallecular vittae which have been mentioned by Bentham[24] as occasionally existing. I thought at that time that the indication of small and "interrupted" vittae might be due to a confusion with spots of waste products, particularly of tannin—which are to be found now and then in the outer parts of the mesocarp. But since that time I have seen a paper of Borde,[25] devoted to *Crithmum*, unknown to me formerly, in which these small vallecular exterior vittae are really described and figured. As is so often the case with anatomists who work without any consideration of physiological functions, the author mentions only in two words, like Geneau de Lamarlière,[26] the enormous development of the "tissu spongieux" (our pleenchyma) and has no idea of its functions; he does not even notice the presence of the layer of disaggregation. On the other hand, he gives a careful study of the evolution and topographical distribution of the vascular bundles in the fruit. I studied after him, using good material, younger mericarps and can now confirm his indications. There are in each vallecule 1–3 minute vittae, located in the chlorenchyma at the limit of the pleenchyma. Except for very rare exceptions, these small vittae are entirely obliterated in mature mericarps; the obliteration is so complete that in

[22] Reichenbach, H. G. (fil.) op. cit. p. 30, 1867.

[23] Drude, O. (In Engler und Prantl) op. cit. p. 201, 1898.

[24] Bentham, G. Handbook of the British Flora p. 254, 1858.

[25] Borde, F. Etude pharmacognosique du Crithmum maritimum L. pp. 40-48, figs. 14–19, pl. 2, Lons-le-Saunier, 1910.

[26] Lamarlière. Géneau de. Recherches morphologiques et phyiologiques sur les Ombellifères p. 125, Paris, 1893.

most cases the sites of the vittae can not even be recognized with the help of powerful clearing agents like chloral hydrate.

<div align="center">PTILIMNIUM NUTTALLII BRITT. (Fig. 7)</div>

<div align="center">(*Discopleura Nuttallii DC.*)</div>

Again we shall consider a species whose mericarps possess 2 marginal floats, presenting very elegant characters. The mericarps have 5 salient ribs; the dorsal and lateral ones are free, while the marginal ribs are laterally united with the floats.

Fig. 7. *Ptilimnium Nuttallii.* Equatorial cross section of the mericarp. *Ep,* epicarp; *Chl,* chlorenchyma; *Ed,* dorsal, *Fl,* lateral and *Fm,* marginal stereom columns each with a vascular bundle on the internal and a secretory canal on the external side; *Bv,* vallecular vittae; *Bm,* commissural vittae; *Pl,* pleenchyma; *Ed,* endocarp; *S,* seed.

The epicarp consists of tabular cells, with thickened exterior walls covered by a strong folded cuticle. The few stomata are small and inserted below the exterior level of the epicarp. Under the whole surface of the epicarp is a thin region of microcytic chlorenchyma. Under the chlorenchyma a small column of stereome is to be seen in each rib, leaning outwards on a weak vascular bundle accompanied by a very small intrajugal vitta. The vallecular vittae are very voluminous and strongly diaphragmed; they are salient as well in the vallecules as in the coelum of the mericarp. The two commissural vittae stand very near each other and are separated from the vallecular ones by the whole breadth of the floats.

The endocarp consists of tabular cells, which in mature fruits are generally much crushed. The 2 floats have in cross section a more or less triangular-ovate shape. The cells of the pleenchyma are polyhedric, often redivided, with angular intercellular aeriferous spaces; the cell walls are lignified, relatively thin, with very numerous pits, which vary in shape from polygonal to roundish and elliptical; the ellipse is sometimes much lengthened and always perpendicular to the great axis of the cell. The resistance to penetration by water is considerable. Floating is effected mostly with the commissural face of the mericarp turned upwards. *Ptilimium Nuttallii* is an inhabitant of swamps.

OENANTHE L. (Figs. 8, 9)

For details relating to the carpology of this very interesting genus, I refer the reader to my paper of 1899. I shall only summarize here the most important features in order to allow a rapid comparison with other Umbelliferae.

The shape of the mericarps in cross section is more or less half circular, with prominent ribs or without any ribs (*O. globulosa* L.).

The pleenchyma is always grouped in floats. In *O. globulosa* L. the five floats, surrounded by a narrow shell of chlorenchyma, are nearly homomorphic, except the marginal ones which extend rather far on the commissural side; they are separated from each other by narrow blades of living parenchyma. The species with more or less prominent ribs have their floats situated in the ribs, the floats in the marginal ribs being much more developed than in the
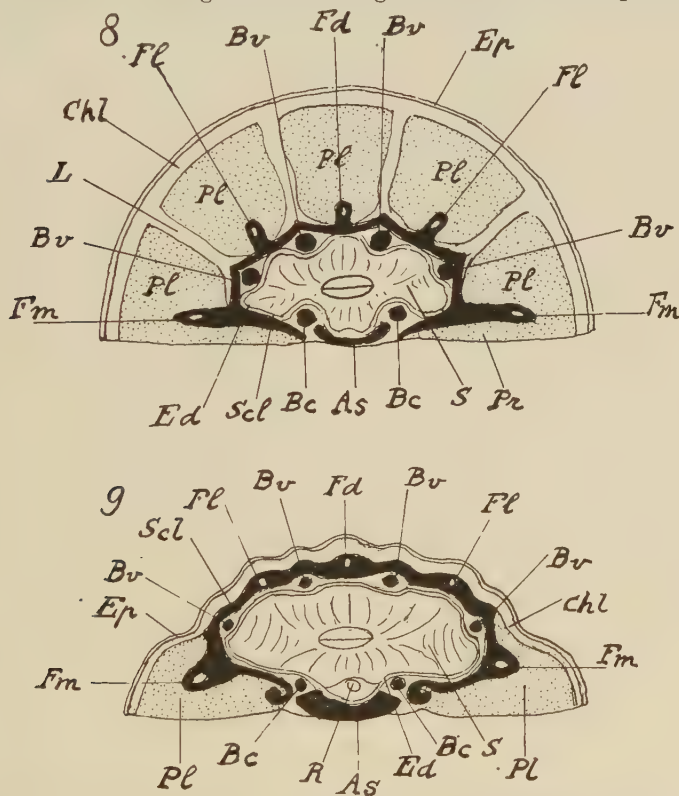
Fig. 8. *Oenanthe globulosa* L. Equatorial cross ection of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Pl*, pleenchyma distributed in 5 floats separated from each other by blades of parenchyma, *L*; *Scl*, sclerocarp; *As*, commissural sclerocarpic bow; *Fd*, dorsal, *Fl*, lateral, and *Fm*, marginal vascular bundles; *Bv*, vallecular vittae; *Bc*, commissural vittae; *Ed*, endocarp; *Pr*, commissural extension of the marginal floats; *S*, seed, endosperm, embryo.

Fig. 9. *Oenanthe pimpinelloides*. Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Pl*, pleenchyma distributed in two marginal floats; *Fd*, dorsal, *Fl*, lateral and *Fm*, marginal vascular bundles; *Scl*, sclerocarp; *Bv*, vallecular vittae; *Bc*, commissural vittae; *As*, commissural sclerocarpic bow; *Ed*, endocarp; *S*, seed, endosperm, embryo.

others; all are separated from each other in deep levels by living parenchyma. In *O. fistulosa L.* the cross section of the floats is lyre-shaped, the branches of the lyres coming in touch with each other. *O pimpinelloides L.* has only two big marginal floats in the mericarp. The cells of the pleenchyma are poly-hedral, more or less rounded at the angles, so as to allow room for small intercellu-lar aeriferous spaces. In several species, the cells of the pleenchyma become more or less stretched radially in the course of the evolution of the tissue, and this stretching is accompanied, especially in the more central elememts of the floats, by tangential divisions, which give to the whole something of the ap-pearance of a periderm, but never so regularly as is the case in *Berula*. In mature mericarps, the cells of the pleenchyma become filled with air. The cell walls remain generally very thin, even at maturity. However, sometimes they become a little thickened (*O. silaifolia* M. B.). In all cases, they are more or less lignified. The negative results obtained with alcannin and the absence of coloration with Correns reagent show that they are not suberized. Never-theless, they are very impermeable to water and air.

The sclerocarp, occupying the inner portion of the mesocarp, presents very variable and interesting features. In all species, there are farthest within 1–4 layers of prostrate stereids. Leaning outwards against them are "erect" stereids making a continuous belt all around the mericarp, except in the com-missural sinus, where the belt is interrupted (*O. globulosa* L., *O. silaifolia* M.B., *O. pimpinelloides* L., etc.). In other instances, there are as many bows of ster-eome as ribs (*O. Phellandrium* L.). The belts or bows of stereome protrude into the floats in many species (*O. globulosa* L., *O. silaifolia* M.B., *O. Lachenalii* Gmel., *O. pimpinelloides* L.), affecting sometimes the characteristic ⊥ form of pillars (*O. globulosa* L., etc.).

The vascular bundles are small and very often imbedded in the stereome in the inner region of the ribs; their exact situation is therefore difflcult to as-certain in mature fruits.

There are 4 vallecular vittae, and 2 commissural ones, all furnished with well developed diaphragms.

The endocarp consists of a layer of parallelipipedoidal, tangentially stretched cells, with inner and outer walls more thickened than the radial ones. These walls are often somewhat suberized; in *O. crocata* L. they assume the characters of collenchyma.

I would have now, after 30 years of carpological work on *Umbelliferae*, several corrections of detail and amplifications to present about the fruit of *Oenanthe*, but that would be here of little interest. The main point is that the fruits in the genus *Oenanthe*, whose species inhabit marshes, lakes, and the sea shore, possess a remarkably developed floating apparatus, which enables them to swim easily on water.

LILAEOPSIS OCCIDENTALIS GREENE (Fig. 10)

In *Lilaeopsis*, the equatorial cross section of the fruit is elliptical (weak dorsal compression) and almost circular towards the extremities, as in *Oenanthe globulosa* L., but with a very different interior structure.

The epicarp is formed of a layer of parallelipipedoidal cells, with moderately thickened exterior cell walls and a smooth cuticle. The few stomata are very small and inserted below the external level of the epicarpic cells.

The mesocarp is entirely leptocarpic and differentiated externally in a microcytic chlorenchyma, which subtends the epicarp on its whole surface. On the dorsal side of the mericarps, this chlorenchyma is immediately followed by a macrocytic parenchyma which extends all around the deeper regions of the mericarp, leaving aside the floats. The vittae are situated in that parenchyma, 1 in each vallecule and 2 in the commissural sinus. All 6 vittae are elegantly diaphragmed. The 5 vascular bundles are small, more or less circular in cross section, and situated at the outer limit of the macrocytic parenchyma, partly fitted in the chlorenchyma. All are flanked externally by a small intrajugal vitta. The endocarp consists of tabular cells, rectangular and tan-
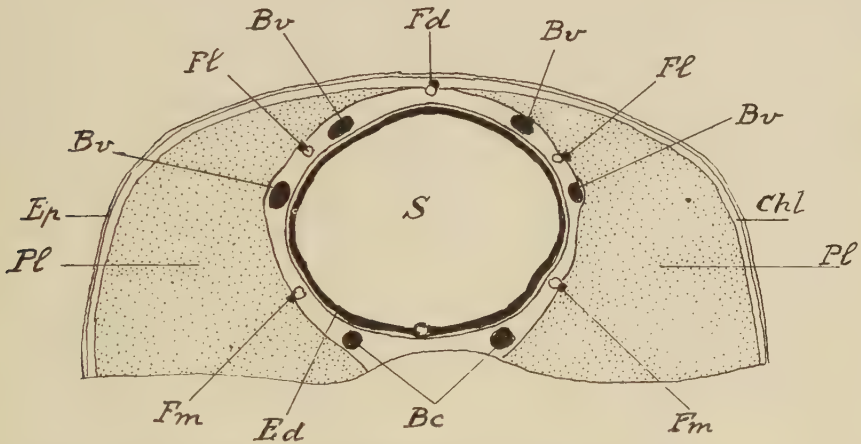
Fig. 10 *Lilaeopsis occidentalis*. Equatorial cross section of the mericarp. *Ep*, epicarp; *Chl*, chlorenchyma; *Pl*, pleenchyma; *Fd*, dorsal, *Fl*, lateral and *Fm*, marginal vascular bundles each with an external secretory canal; *Bv*, vallecular vittae; *Bc*, commissural vittae; *Ed*, endocarp; *S*, seed.

gentially stretched in cross-section. The cell walls are stiff, somewhat suberized, with a tendency to the formation of Caspary's specks on the radial walls: the endocarp functions, as is the case in many Umbelliferae, as a kind of endodermis with reference to the endosperm and the embryo which fill up the whole coelum of the mericarp.

The two large sized floats are marginal. Their volume surpasses considerably the volume of all other tissues of the mericarp; they look as if they had been carved out of the flanks of these tissues. Their pleenchyma consists of polyhedric cells with angular aeriferous intercellular spaces; they are relatively small, owing to the abundant and irregular redivisions of their far less numerous mother cells; as soon as these divisions are achieved, the cell walls lignify, the protoplast dies, and the cells become filled with air. The cell walls are very thin, smooth, or with few and very minute pits. Here also the great imper-

meability seems to be owing to the migration of some insulating substance into the cell walls. The characteristic of these floats is their great lightness.

The mericarps float with either the keel or the commissural face (the "deck") turned upwards, as is the case in *Oenanthe*. This very elegant and effective floating apparatus corresponds admirably to the aquatic or subaquatic habits of *Lilaeopsis*.

III

The question which arises unavoidably when studying the organization of the floating apparatus of aquatic and littoral Umbelliferae and inquiring into its manner of acting in nature is this. How has this apparatus primitively, been formed? How has it become proper to the species which bear it? It is a concrete case of the old problem of the origin of adaptations.

Adaptation! The term is nowadays little in vogue, "peu à la mode". Nevertheless I continue to use it in its etymological sense (*aptus ad, aptatus ad*), for it expresses a reality characteristic for all living beings. An organ is adapted to a function when it is built in such manner as to fulfil that function. A plant, that is, a harmonic ensemble of organs, is adapted to a medium, when these organs correspond by their structure to the requirements of that medium, when the plant is apt to live in that medium. Adaptation, in the objective sense of the term, is an absolute necessity; without adaptation, life would be impossible. The study of adaptations connects morphology with physiology in the broadest sense of these words and constitutes for itself a special branch of science: ecology. But it is important to make a clear distinction between the facts of adaptation, that is the objective constatation of a relation between structure and function, from the theoretical explanation which we can try to give in respect to the origin of these phenomena. It is always possible to state the reality of an adaptation and it is often possible to study its modalities experimentally, without leaving the solid ground of objective science. That imagination may lead the observer into error, in this domain as in so many others, does not constitute a serious objection against the study of adaptations. Hypothesis has always been and will always remain a capital instrument of progress, and nobody would consent not to make use of it. The essential point is to subdue imagination to a constant critical spirit. Moreover, if an author does not exercise criticism to a sufficient degree upon his own interpretations, others will rapidly do it for him, so that finally, some times slowly and with frequent returns and vicissitudes, the truth will have the upperhand.

If we can therefore consider quietly the future development of the study of adaptations, things present themselves very differently as concerns their origin. Actually the theories which have been proposed, from Lamarck and Darwin down to our contemporary biologists, have little more value than the expression of a belief, at least to a certain extent. I say "to a certain extent", because the reasons which we have for accepting a solution must be exclusively taken from objective facts, which confines "belief" in certain definite limits.

That does not at all mean that a scientist has no right to construct his own metaphysical philosophy, but he must never forget that this philosophy, of whatever kind it may be, does not belong to science and must not be allowed to interfere with his scientific judgements.

In this sense, my hearers or readers are free to consider the following considerations as a kind of "creed". It is useful and perhaps suggestive that now and then a botanist should define the point of view to which he has been led by his research and by his thought.

Let us note at first that the floating apparatus of the fruit in Umbelliferae is useful, but that it is not possible to pretend that it is necessary. Various aquatic or subaquatic Umbelliferae show fruits organized in such a manner that one hesitates in ascribing the function of floating to an apparatus, which is, in this respect insufficiently differentiated. Far more, there are aquatic or littoral Umbelliferae which have certainly no floating apparatus in their mericarps, the fruit being besides that destitute of any other special means of dispersal. I could cite several examples of that kind. One of the most striking is furnished by *Ottoa oenanthoides* H. B. K. In this plant the vegetative parts show one of the most remarkable and rarest modifications related to aquatic habitat which is to be found in Dicotyledons: rush-like, juncoid, articulated and diaphragmed leaves, as in *Lilaeopsis, Oxypolis teretifolia, Thorella*, etc.[27] Now, the fruit of this species, in contradiction with what one might expect, presents no vestige of a floating apparatus. It is therefore impossible to establish a *constant* and *necessary* relation between the aquatic or subaquatic conditions of life and the presence in the fruit of a floating apparatus in Umbelliferae, hence no direct relation from cause to effect between environment and the special organs here studied.

If the *necessity* of a floating apparatus for aquatic or littoral Umbelliferae— and the same holds for very numerous adaptational characters in relation with the dispersal of fruits and seeds—cannot be avowed, on the other hand, their *utility* is unquestionable. It is beyond doubt that, lacking a flying apparatus, the bearers of fruits with a floating apparatus are advantaged when compared with Umbelliferae of analogous ecological habits, yet having no such apparatus. Most of the hydrophilous continental species possessing a floating apparatus in the fruit, which we have studied, extend over great areas; the halophile maritime ones have a dispersal attaining great distances. For example, *Crith-*

[27] On the morphology, anatomy, and ecology of these plants with diaphragmed leaves see: Goebel, K. Pflanzenbiologische Schilderungen. 2: (cf. p. 45.) Marburg, 1891; Bitter, G. Vergleichend-morphologische Untersuchungen über die Blattformen der Ranunculaceen und Umbelliferen. Flora 83: (cf. p. 272.) 1897; Goebel, K. Organographie der Pflanzen. p. 494. Jena, 1900; Briquet, J. Recherches sur les feuilles septées chez les Dicotylédones. Bull. Herb. Boissier. Ser. 1, 5: 453–468; et Bull. Lab. Bot. gén. Univ. Genève. 1: 264–279. 1897; Rennert, R. J. The phyllodes of Oxypolis filiformis, a swamp xerophyte. Bull. Torr. Bot. Club. 30: 402–411. 1903; Briquet, J. Thorella, Ombellifère monotype du sud-ouest de le France, étude monographique comprenant des recherches nouvelles sur les phyllomes septés des Ombellifères., Ann. Cons. et Jard. Bot. de Genève. 17: 235–277. 1914; Chodat, R. La végétation du Paraguay. Ombellifères. Bull. Soc. Bot. de Genève, Ser. 2, 12: 27–31. 1920.

mum maritimum, a rupicolous halophile, is to be met not only on all the coasts of the Mediterranean, but also in most of the small islands, provided that the conditions necessary to its vegetation be realized; beyond the strait of Gibraltar, *Crithmum* extends along the western coasts of Europe as far as the South of England and reaches even two localities in Southern Ireland; finally, the species reappears in the group of the Azores, at Madeira and in the Canaries.

Under these conditions, the problem becomes very complex. We have to do with *useful* but not *indispensable* organs; they are undoubtedly related to a special mode of life (the aquatic one), and yet they cannot be considered as a necessary response to the stimulus of environment. Without entering into the inextricable discussion of the possible heredity or non-heredity of acquired characters, it is obvious that the entirely hereditary floating apparatus of the fruit in Umbelliferae has nothing to do with the characters of accomodation of the vegetative parts of plants which are in direct contact with aquatic environment, whether these characters be reversible or not. To what kind of hypothesis can we then have recourse if we try to form a representation of the origin of the floating apparatus?

I would personally try to give an answer based on the following considerations.

Orthogenesis is a principle whose realization in the phylogenetical history of living beings seems to me fundamental. The successive changes in organs are doubtless effected along definite lines, because these lines are determined by the structure of the germinal plasma itself. No taxonomist will escape the reality of the orthogenetic process. I only recall the classical examples of Gymnosperms whose evolution since the paleozoic times down to the present day has been effected through all vicissitudes of climate and geographic changes in a definite direction; of the tertiary American horses with the gradual, regular reduction of their toes. In ordinary systematic work orthogenesis imposes itself with no less strength when studying parallel series, homologous groups, etc. The characters inherent to orthogenesis are called *phyletic* by taxonomists. Besides these phyletic characters, and in opposition to them, the *epharmonic* characters, which are also hereditary, are in relation with environment. I use here the term *epharmonic* in a rather broader sense than Vesque, its creator. The floating apparatus of the fruit in aquatic and littoral Umbelliferae is for me an epharmonic character because, by means of modifications in tissues which to varying degrees all members of that family possess, this character renders the plants more closely apt to dispersal by water.

The distinction which we establish between phyletic and epharmonic characters, however convenient it is in practice, is of course no absolute one. Certain characters which are actually considered as purely phyletic may have been epharmonic at the beginning, but their origin can no more be ascertained because it loses itself in the past. On the other hand, taxonomists are accustomed to reckon with the *epharmonic behavior* (allures épharmoniques) of a group, which finally gets integrated in orthogenesis.

We thus assist to an *entangling* of orthogenesis and adaptation, of phyletic and epharmonic characters.

Such is the case for the Umbelliferae which we have studied: the floating apparatus, an epharmonic character, has been incorporated into the hereditary patrimony of various genera, and in genera with numerous species (*Oenanthe*), it has become differentiated so as to show a particular behavior in the different sections of the genus.

I cannot ascribe to hazard-mutations in the histotaxy and histology of the fruit, the origin of the carpic floating apparatus, for that would be not only purely hypothetical but also destitute of any known example either of observation or of experiment. This precise case, among thousands of others furnished by the vegetable world, shows the complete insufficiency of the ordinary mutation theory as soon as one steps into the domain of adaptation. Cuénot has confessed it recently in his cleverly written book on adaptation[28]: Mutationism rejects, says he, Lamarckism and Darwinism; it denies the heredity of characters acquired by the soma and the constructive rôle of natural selection: "Mais il n'a rien de plausible à proposer à la place; il faut avouer qu'il manque quelque chose à nos conceptions de l'évolution et de nos facteurs; la nécessité d'un facteur nouveau, interne ou externe aux organismes, régulateur des variations et capable de les diriger vers une fin, se fait surtout sentir lorsqu'on étude des organes complexes comme les yeux, les organes électriques . . . . . etc."

It is in no way my intention to propose here some new theory to be added to the very numerous ones with which we have already been blessed. However I deem it worth while to insist upon a consideration which is not new at all but to which no sufficient importance is generally given: that is the indirect action of the environment upon the germinal plasma of the egg *through the intervention of the soma*. Let us suppose that the conditions in which the soma lives are new ones, supportable for it, followed by some of the ordinary processes of accomodation; then these new conditions will necessarily bring changes in metabolism and provoke changes of structure in all degrees of the morphological hierarchy: organs, tissues, cells. This is no theory, but a result of observation and of experiment. The germinal plasma will now be placed in a new internal, somatic environment. It is impossible, not only from the biological but also from the physico-chemical point of view, to admit that such a situation protracted during immense periods of time, could be of no effect upon the germinal plasma itself. We have become accustomed of late to localize exclusively the seat of heredity in chromosomes, but I personally doubt very much that this absolute view will be definitive. If it be true that elements of the egg, other than the nucleus, for example chondrioms, divide independently of the nucleus, and are bearers of hereditary characters (transmission by division of chondrioms of such characters as color), it must be owned that the facts of heredity are still far more complex than we can imagine. Now,

[28] Cuénot, L. L' Adaptation p. 155, 156 (Encyclop. Scientifique Bibl. de biologie générale. Paris, 1925).

nothing prevents us from admitting that modifications, obtained in the manner above alluded to, in the germinal plasma should have as a consequence the initiation of mutations in relation with the new altered conditions of the soma, and hence with the external conditions of environment. In that way epharmonic characters could be incorporated into orthogenesis (itself a fundamental property of living substance whose mechansim is and will perhaps always remain unknown). A solution might be sought in future in that direction. It is to be feared, however, that for a long time to come, all this will not go farther than ingenious speculations, for the great obstacle resides in a factor often despised by theoretists and by genetists, and which is capital: this factor is *time*. We can call *time* to interfere in our laboratory research and in our cultural experiments only in an infinitesimal manner, which is quite out of proportion with the rôle which it has played and plays in the vast laboratory which we call Nature.

I would thus conclude by approving the judicious thoughts recently developed by Reinke[29]. I would say: Let us continue actively research work in the laboratory; let us persevere in utilizing the resources which our great herbaria put at the disposal of taxonomy; let us multiply genetical studies and culture experiments; but let us never forget that nature is the laboratory *par excellence*. Let us, therefore, come out of our small special compartments in which the horizon is necessarily limited *in time and in space*, to take frequent and intimate contact with life as it manifests itself in the free nature.

[29] Reinke, T. Ueber Botanisieren. Ber. der deutschen bot. Gesellsch. **43**: (Schlussheft) **19–25**. 1926.

THE TAXONOMIC TREATMENT OF UNITS SMALLER THAN SPECIES[1]

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Of the making of species there is no end. The total number of plant forms, including true species and their variations, is so vast that it will require many future generations of taxonomists to name and describe them, notwithstanding the splendid start already made.

If any one imagines that the end is in sight he need only to make a monographic study of almost any of the larger genera, or even of a collective species, and combine this with extensive field studies, to be entirely disillusioned. Under such scrutiny old and well-established taxonomic units crumble into fragments. Without multiplying examples, reference need be made only to such studies as those of Clausen on *Viola tricolor*, of Greene on the American species of *Viola*, or of Turesson on *Atriplex, Solidago*, and numerous other genera. The cases of *Rosa* and *Hieraceum* come also to mind, while among cultivated plants may be noted the 500 or more varieties of *Triticum aestivum*.

The systematist of today, recognizing the overwhelming multitude of these natural forms, is confronted with the problem of their proper taxonomic disposal. If his task is to be completed, he must ultimately account for all of them, no matter how small or seemingly insignificant. There may be justifiable doubt as to the advisability of carrying classification to this extreme at the present time, but there can be no doubt that the task falls within the province of taxonomy and that its completion is an ideal to be kept clearly in mind.

The difficulties encountered in the treatment of units smaller than species have to do chiefly with minor divisions. The relationships, and hence the classification of the larger ones, often may be worked out with considerable satisfaction. These are the subspecies of many authors, more especially those of Europe. The term variety is frequently used for this primary division of the species, notably in America, but the term has such a multiplicity of uses and so often applies only to races, ecologic responses, horticultural forms, or even to abnormalities that, in the opinion of the writer, its use in serious taxonomic work were better discontinued.[2] But while relationships and the resulting classification of the subspecies may give no serious trouble, notwithstanding many apparent intergrades and natural hybrids, the taxonomic disposal of the smaller

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 18, 1926.

[2] The author sees no objection to the use of the varietal category for the unit next below that of subspecies in cases where the classification has been determined by experimental or other precise methods.

units always is a baffling problem. This is due in part to the frequent mixing of their hereditary traits, resulting in innumerable character-combinations, and in part to our inability to determine from morphologic studies alone which characters are heritable, namely, genetic, and which are only temporary responses to the environment.

Up to the present, three principal methods for the handling of these important but annoying forms have been proposed. The first and simplest is to treat all of them as full species. This involves a shifting in the time honored concept of species. Lotsy has gone even so far as to propose that the original species, that is, such as those of Linnaeus, now be called Linneons and that the smaller forms be classed as Jordanons if gametically impure, or as true "Species" if gametically pure. It should be noted, however, that this is merely a shuttling of words and that if the rule of priority is involved, that rule which makes 1753 the starting point for nomenclature, then Lotsy's "Species" is a homonym and his word "Linneon" is synonymous with the earlier word, species!

More serious objections to the degradation of the species concept are found in the difficulty of recognizing the smaller units, and, in most cases, in the absence of a clear separation between them. There is also to be noted the overwhelming number of resulting binomials, detached names which apply to small units and tell little of their relationships. On the other hand, the essential criteria of a true species are that it shall be a natural assemblage of forms, that is, a true phylogenetic unit; that it be well separated from its neighbors; and that it furnish a practicable working basis.

A second method of handling segregates is to organize them into various categories, such as subspecies, varieties, subvarieties, forms, subforms, etc. This is a logical disposal and has a strong appeal to lovers of system. Its weakness lies in the unwieldy combinations that result and, what is much more serious, in the fact that dependable criteria for such elaborate groupings are almost always lacking. The system becomes absurd when carried out in the herbarium, for the result is then merely an expression of opinion based upon scant evidence; whereas its justification must rest primarily upon evidence to be obtained only by field studies and especially by field and garden experiment. Moreover, the evolutionary lines leading to these small units make so complicated a network that natural relationships cannot be expressed in the arrangement of names.

The third method for the disposal of small units is to describe them only in a numbered or lettered list of minor variations and to leave them in this provisional category until their status can be determined by experimental and other exact methods.[3] This disposal is the one particularly favored by the writer. It is recommended because it does not compel the systematist to commit himself when evidence is lacking, and because the genetic complexities between the forms usually are too great to be expressed by names or their arrangement. It is a practicable method, the only one which permits of accounting for all

[3] Examples are to be found in Hall and Clements, Phylogenetic method in taxonomy. Carnegie Institution of Washington Pub. **30**: 1923.

of the forms without beclouding species and subspecies concepts. It permits of numbering or lettering the forms and even of diagramming supposed relationships or artificial groupings. Especially noteworthy in this connection is the grouping of character-combinations, as illustrated by Clausen in connection with the forms of *Viola tricolor*, and the working out of systems of the minutest systematical units, varieties, and races, as proposed by Vavilov. If need arises, as in genetics or horticulture, special or fanciful uninomials may be applied without upsetting the nomenclature of the larger taxonomic units, and without introducing false concepts as to relationships. Familiar examples are the horticultural varieties of roses and apples, the cultivated races of wheat, and the genetic segregates of *Oenothera lamarckiana*.

Here, then, these minor variations may be left until such time as they are taken up by the specialist working with more refined tools than now lie at the hands of most taxonomists. But this does not complete the task of the systematist. To him, more than to any of his colleagues, falls the task of finding new methods for arriving at an understanding as to the nature and relationships of small forms and the part they play in the evolution of his larger units.

Various new methods are now being discovered and utilized, especially those of geographic distribution and ecologic behavior on the one hand, statistics and chemical reactions on the other. Cytology, also, is opening up a new field, especially as regards chromosome characters. But the most promising field, namely that of direct experimentation, has been left almost entirely to the geneticist and the ecologist.

It is of opportunities in this experimental field that I wish now to speak, for I am convinced that detailed experimental studies should precede any serious attempt to classify the smaller taxonomic units.

The first grouping of the minor variations that suggests itself is into heritable and non-heritable forms. Taxonomists often fail to distinguish between these categories and, indeed, it often is impossible to determine by observation alone whether a certain feature is the result of heredity or only a temporary ecologic response. Many botanists, from Kerner and Bonnier down, have devised experiments to test particular forms as to this point, but the most extensive work has been carried out by Turesson, working in southern Sweden. By moving perennial transplants of closely similar forms into a uniform habitat and noting whether or not they then become alike, this experimenter aims to determine whether the original forms were genetic types or modifications due merely to environment. The former, namely, forms which retain their characters despite changed environmental conditions, Turesson classes as ecotypes and he is now building up a classification of these based upon the ecologic conditions to which they are suited. He thus has a classification of minor variations into (1) modifications, which are not further considered, and (2) ecotypes, such as oecotypus *campestris*, oect. *salinus*, oect. *subalpinus*, oect. *alpinus*, etc.

Such experiments are of first importance, since they yield definite results as to the nature of the forms. Also, they furnish the first step in the rational classifications of minor variations. It is suggested, however, that the number

of ecotypes of even a single species may be very great, and that apparently identical ecotypes from widely separated places may be of diverse origin, so that a complete classification may be beyond the reach of practicability.

Transplant experiments for the testing of minor variations, and of taxonomic criteria generally, have been in progress at the University of California and at the stations of the Carnegie Institution of Washington for many years. Here methods have been developed by MacDougal, by Clements, and by the writer.

The more promising of these experiments may be classed into six groups:

1. The transplanting of similar but unlike forms of perennial species into a uniform environment. Thus, for example, related forms from high, medium, and low altitudes may be brought into gardens at a moderate altitude and observations made as to convergence in feature or its absence. Or, more simply, sun and shade forms, or edaphic variations, may be grown under uniform light and soil conditions. The majority of Turesson's transplants are of this class.

2. The transplanting of a single perennial form into diverse environments. This is for the purpose of testing the stability of characters and to determine whether or not a form can be so modified as to resemble other related forms. Since apparently identical plants may be unlike genetically, the best results are obtained when an individual is divided and the parts carried to the various transplant stations. This is especially important if there is contemplated the genetic testing of resulting changes. Difficulties due to what the geneticists call bud mutation are overcome by running several parallel experiments and discarding the results when these are not uniform.

3. The use of reciprocal transplants. By this method two related perennial forms, growing at different places, are interchanged, each being planted in the exact spot from which the other was taken. This is an attractive but a difficult method, for it necessitates the maintenance of transplants under natural conditions, often at considerable distances from each other, and where care and protection may be impossible. Reciprocal transplants have been established, however, between certain Rocky Mountain plants and the corresponding forms in the Sierra Nevada of California. Successful reciprocal exchanges have been effected also between the Sierra Nevada, at 3000 m., and the coast of California at under 200 m. Some reciprocals are much more easily made, as between forms from opposing sides of a cañon, or between sun and shade forms.

4. Habitat inversion. Strictly speaking, this is not a transplant experiment, for instead of moving a plant into a new environment, the plant itself is left untouched while the environment is changed or inverted. An example is the removal of the shade from a plant growing beneath copses.

[In all of the four foregoing methods, only perennials are used. The experiments are repeated with as many individuals as practicable, but vouchers are preserved in the form of herbarium specimens (and often liquid material for histological study, as well as photographs) of every individual moved.]

5. The growing of seedlings of related annual forms under uniform conditions. For this, it is better to start with genetically tested homozygous material,

but if uniform results are obtained from a large series of seeding experiments the evidence may be accepted as conclusive.

6. The growing of seedlings of a single annual form, under diverse conditions. Here, also, genetically uniform seed is preferred, but such seed is rarely available. Seed may therefore be gathered from wild plants if care is taken to see that the results at each station are practically uniform.

Additional types of transplant experiment are now in process of development.

Results are sometimes immediately obtained from transplant experiments but usually they yield returns only after many years, if at all. Time must be given for the plant to become established in its new home and to escape the influence of its former habitat. Then, if it is assumed that the effect is cumulative, time must be allowed for the new influence to act. Bonnier has reported changes that became noticeable only after periods of 10 to 15 or more years but he furnished no satisfactory evidence of this. It would be very desirable to have his experiments repeated with proper modern controls and safeguards. Especially important is the protection against invasion by seedlings and the institution of methods to insure the identity of individual plants. In such work it is also essential to have vouchers in the form of herbarium specimens and photographs, preferably taken annually.

In our own experience there are numerous cases where characters have been modified in the first or second season but none in which changes can be positively said to have occurred after the second year. This persistence of a form or character, regardless of the conditions to which it is subjected, may be taken as suggesting but not proving its hereditary or genetic nature. Whether or not it should be taken as of specific value in taxonomic work is an entirely different question.

Detailed reports will be given elsewhere but a few selections may now be presented to illustrate the methods employed.

1. Variations of the herbaceous *Artemisia vulgaris* subsp. *heterophylla* brought from the seashore, from the lower hills, and from the mountains at 1500 m. altitude retained each its own peculiar cut of leaf when grown under uniform conditions for a period of years. Thus these are seen to represent hereditary types (ecotypes) although too trivial for classification as subspecies. Numerous other ecotypes of *A. vulgaris* are now demonstrable in the cultures, as well as myriads of minor variations which are immediately modified by the environment.

2. *Solidago elongata*, when grown in partial shade, bears all the heads in narrow, compact, spike-like panicles. When an individual is divided and a portion transplanted to a near-by plot, fully exposed to the sun, every stem branches to make an open, spreading inflorescence, each branch of which is comparable to the entire panicle of the shade form. The exact cause of this modification is not known, but the experiment demonstrates that in *Solidago*

the ecologic factors sometimes control the degree of branching, and hence the appearance of the inflorescence.[4]

3. *Symphoricarpos albus*, grown in the shade, produces an abundance of broad, deeply lobed leaves. Portions of the same plant (individual) grown in the sun produce smaller, mostly entire leaves. The amount of lobing is used as a specific criterion in the taxonomy of this group but lobed leaves are especially characteristic of young stems and sterile shoots. It seems, therefore, that reduced light, through modification of development, may give to one taxonomic "species" the aspect and perhaps the characters of another.

4. *Hemizonia congesta* subsp. *clevelandi* has been characterized as distinct from subsp. *luzulaefolia* mainly on its spicate inflorescence. (The two are accepted as distinct species by most authors.) Seeds of uniformly spicate plants were grown under different conditions of moisture. Seedlings in dry soil yielded only spicate inflorescences; those in moist soil had branched, paniculate inflorescences; those in soil moderately moist produced intermediate types of inflorescence. These experiments, repeated at 3 stations and also in pot cultures gave uniform results. The modifiability of the inflorescence character is thus proven, but since it is correlated with other characters which apparently are not modifiable, its use in classification may still be of service.

5. *Madia elegans* has ligules which are typically pure yellow but in a common form each ligule has a prominent maroon blotch at base. Seed gathered from a colony of pure yellows gave plants uniformly of this type. Seed from a colony in which all of the plants had ligules with a maroon blotch gave plants with uniformly blotched ligules. Seeds were also gathered from a colony where the two forms grew intermingled, but the seeds of each form were kept separate. Those from the pure yellow form yielded only plants of this type; but those from the form with maroon spots gave both kinds of offspring. This demonstrates that the presence or absence of the maroon blotch is a heritable trait; that its presence is dominant to its absence; that the colony of pure yellows was composed of homozygous recessives (as to this character); that the colony in which all the ligules were blotched was composed of homozygous dominants; and that the mixed colony was composed of homozygous recessives (yellow), homozygous dominants (maroon), and heterozygous dominants (maroon).

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[4] The modification is now known to be the result of injury to growing tips through action of an insect restricted mostly to sunny situations.—H. M. H. 1930.

Fig. 1–7. Variations in transplants. 1. *Hemizonia congesta* ssp. *clevelandi* 2. The same, but from a plant grown in drier soil. 3. Head of *Madia elegans*, the ligules pure yellow. 4. Head of *Madia elegans*, each ligule with a maroon blotch at base; the blotch is a heritable character, and its presence is dominant to its absence. 5, 6, 7. Forms of *Artemisia vulgaris* ssp. *heterophylla* from interior mountains, coast ranges, and seacoast, respectively, each holding its characters when grown in a uniform environment.

Fig. 8–11. Variations in transplants. 8. *Symphoricarpos albus* grown in full sunlight. 9. A division of the same plant, but grown in shade. 10. *Solidago elongata* grown in full sunlight. 11. A division of the same plant, but grown in half shade.

THE DATA OF SYSTEMATICS AND THE ORDER OF FLOWERING[1]

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The idea I wish to present here is that the order of the flowering of plants during a summer coincides with the order of their phylogenetic evolution. It is well known which types of plants are the most highly developed (or later) ones,—plants with synpetalous flowers, with the synsepalous (united) calyx, with the inferior ovary, with a single circle of stamens, and as a representative family I might cite the compositae. The percentage of the flowering of these "superior" types, as is well seen in the tables appended (Tables 1–3), gradually and ceaselessly increases from the beginning to the end of summer, that is, flowers appear and begin to prevail during the summer in the same order as they did during the geological periods. In obtaining this evidence I[2] observed the process of flowering during nine years (1917–1925), noting, as much as it was possible, all the wild flowering plants that I found in the local flora (Poltava, 49° 35′ N and 52° 15′ E from Ferro).

Thus during one summer I noted 450 to 500 or more species of flowering plants. For each month I calculated the percentage of the superior types as compared with the general quantity of all the plants in flower (see tables).

My explanation of this law is that the superior—the later—types have a more complex structure, not only externally, but also internally, and therefore they require for their maturation and flowering a longer time and a greater quantity of warmth than the simpler plants, such as the Choripetalae, etc.

I think that my method of controlling the systematic data by observations on the order of flowering of plants may be used in some controversial questions of the evolutionary history of plants.

It would be very interesting to test this law in tropical lands where one vegetative period is not separated from another, and also generally in other latitudes.

Many a species blossomed during many months, therefore there is repetition in the notes, and the common total for the summer is less than the sum of all the monthly data. August does not follow the law closely (due to the flowering of the Chenopodiaceae and other inferior types, also the second (fall) flowering of the spring—primitive—types).

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca New York, Aug. 18, 1926.

[2] See Illichevsky, S. "Journal of Russian Botanical Society" (with French résumé) **9**: 1924. (Leningrad)

TABLE 1. THE NUMBER OF SPECIES OF PLANTS FLOWERING DURING EACH MONTH OF 1923.

Months	No. of species flowering	With inferior ovary		Sympetalae		United calyx		One circle of stamens		Compositae	
		No. flowering	% flowering	No. species	%	No. species	%	No. species	%	No. species	%
Dicotyledons only											
April	45	5	11.0	11	25.6	16	35.5	19	42.2	2	5.0
May	164	22	13.4	47	27.4	69	42.0	61	37.0	8	5.0
June	209	55	26.3	86	41.0	139	66.5	103	49.3	22	10.5
July	155	64	41.3	84	54.0	128	82.6	111	71.6	36	23.2
August	78	29	37.2	40	51.0	56	72.0	46	59.0	20	25.5
Entire summer	425	113	26.6	181	44	187	44	122	28.7	60	14.1
All angiosperms											
April	46	6	13.0	11	22.0			20	45.6	2	4.3
May	166	24	14.5	48	29.0			75	45.2	8	4.8
June	213	59	27.7	86	40.4			128	61.0	22	10.3
July	157	66	42.0	84	53.5		.	123	78.4	36	23.0
August	78	29	37.2	40	51.4			46	59.0	20	25.6
Total per summer	503	120	22.7	182	36.2			187	37	60	11.9

TABLE 2. NUMBER SPECIES BLOSSOMING IN 1924, MONTHLY IN ORDER OF EARLIEST BLOSSOMING

Months	No. of species flowering	With inferior ovary		Sympetalae		Jointed calyx		One circle of stamens		Compositae	
		No. flowering	% flowering	No. species	%	No. species	%	No. species	%	No. blossoming	% of all flowering
Dicotyledons only											
April	23	4	17.4	3	13.0	10	43.5	10	43.5	2	8.1
May	120	17	14.2	29	24.1	57	47.5	43	35.8	8	6.6
June	147	60	40.8	71	48.7	115	78.2	88	58.8	29	19.7
July	41	26	63.4	26	63.4	34	82.9	37	90.2	18	43.9
August	22	11	50.0	10	45.4	13	59.1	19	87.3	8	36.4
Entire summer	353	118	33.4	139	39.4	229	64.8	197	55.8	65	18.4
All angiosperms											
April	29	4	13.8	3	10.3			10	34.5	2	6.9
May	149	19	12.7	32	21.5			63	42.3	8	5.3
June	176	62	35.2	71	39.2			111	63.1	29	16.5
July	48	26	54.2	26	54.1			42	87.5	18	37.5
August	23	11	47.9	10	43.5			20	87.0	8	28.2
Total per summer	425	122	28.7	142	33.4			246	57.3	65	15.3

The calculation of flowers with the zygomorphic and with simple perianth has given no illuminating results.

Another method of calculation was employed whereby I divided the vegetative period into intervals, the sums of the daily mean temperatures of each interval being 500°, so that the first interval included that from 0° to 500° (C), the second from 500° to 1000° etc.—until the sum was 2500° from the beginning of the vegetative period, after which no new flowering plants could be found. The results are given in table 3.

TABLE 3.   THE DATES OF FLOWERING, DISTRIBUTED BY SUMS OF TEMPERATURE INTERVALS
(SUMMARY FOR SEVEN YEARS OF OBSERVATION, 1917–1923)

Periods and sum of temperatures	No. of species in bloom	With inferior ovary		Sympetalae		One circle of stamens		Compositae	
		No. flowering	% of flowering	No. species	%	No. species	%	No. species	%
Dicotyledons only									
I (0°–500°)	129	17	13.2	33	25.6	54	41.8	3	2.3
II (500°–1000°)	189	41	21.7	80	43.4	92	48.7	17	8.3
III (1000°–1500°)	124	48	38.8	66	54.0	84	67.7	30	24.0
IV (1500°–2000°)	65	36	55.4	36	55.4	51	78.5	21	32.3
V (2000°–2500°)	17	13	76.5	8	47.1	15	88.2	6	35.3
Summary	524	155	29.6	223	42.5	296	56.6	77	14.7
All angiosperms									
I (0°–500°)	150	19	12.7	34	22.7	62	41.3	3	2.0
II (500°–1000°)	244	47	19.2	82	33.6	139	57.0	17	6.9
III (1000°–1500°)	149	49	32.9	66	44.3	101	67.8	30	20.1
IV (1500°–2000°)	73	38	52.1	38	49.9	57	78.1	21	28.8
V (2000°–2500°)	20	13	65.0	8	40.0	18	90.0	6	30.0
Total	636	165	25.9	226	35.5	374	58.8	77	12.1

We thus see that all the methods of calculation have given the same results, whichever type is taken as the later one.

The results are even more illuminating in the form of diagrams.

SECONDARY (AUTUMN) FLOWERING AND ITS CAUSES IN CONNECTION WITH THE CAUSES OF FLOWERING GENERALLY[1]

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ABSTRACT

Here I mean to give only the results of my study of secondary (autumn) dowering, which I conducted during eight years by observing conditions in nature and by collecting facts from the literature.

The secondary (autumn) flowering of spring-flowering species is a very common and often observed phenomenon of temperate latitudes. The list I have composed includes approximately 250 species in which secondary flowering was definitely observed in Russia, and nearly 200 other species which seem to have it. Very often it is observed as a "mass" phenomenon, and many species display it every year.

The reason for the phenomenon is found in a transference of the flowering period from the spring to the previous fall, at which (last mentioned) time the buds and blossoms open which normally would open during the following spring. It concerns special buds, branches, and sprays as much as whole plants; examples of such change of season, as well as the reverse transference from autumn to the following spring, can often be observed.

Such shifting of the season, in most cases, can be connected with showers or rainy seaons, often with a particular precipitation. This I was able to determine by the method of temperature sums, but generally the reason of each dowering—the first as well as the second—is a sudden abundance of foods and energy which the plant has no time to use gradually; in other cases they are used for the growth of the vegetative organs.

Vegetative growth and blossoming are antagonistic. In one sense light has a similar effect, for it retards vegetative growth and consequently incites flowering. The same result follows mowing or cutting off the tops of plants; evaporation is thus suddenly diminished, and this leads to an abundance of sap or juices.

Some families of plants do not blossom secondarily at all, or do so very seldom. The following are examples: the orchids, with no case of secondary flowering; the Liliiflorae, rarely with secondary flowering, except Juncaceae; the Amentaceae; and generally those trees which blossom without leaves. Such trees use their excess sap in the unfolding and development of the leaves, so that there is no occasion for a sudden abundance of unused juices, which can occur only in the spring. The first two groups have very feeble roots, which cannot reestablish the conditions lost during flowering. The same is also true of ephemeral spring plants, such as Ficaria, etc. Hence, by analogy, it is not that annuals have very feeble and simple roots; but, on the contrary, plants with feeble and simple roots must be annuals.

SOME FACTORS INFLUENCING THE POPULARITY
OF TAXONOMIC BOTANY[1]

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For some time American taxonomic botanists have felt that taxonomy is not occupying the place in science and education in this country that it should. A questionnaire sent out recently by a committee of the Systematic section of the Botanical Society of America indicated clearly the belief among a large number of botanists and educators that the taxonomic phase of botany should be receiving more attention than at present, and especially that more taxonomic training is desirable in the practical phases of the plant sciences. The reasons for the lack in esteem in which taxonomy is held, as given in the replies to the questionnaires, were very numerous, and doubtless many causes are at work, some economic, some scientific; but a very general feeling appears to exist that taxonomy, though clearly of fundamental importance in plant study, has fallen into a bad way in recent years and has become to a large extent unscientific, or at least impractical. Confusion in nomenclature, in genus and species limits, in phylogenetic concepts as affecting classifications, and the existence of a self-advertising type of taxonomist, or self-styled taxonomist, are cited as evidence of this decadence.

Undoubtedly these accusations are, in a measure, true. The confusion in nomenclature has led to a very sincere desire on the part of many botanists at this meeting to improve the deplorable condition resulting from lack of uniformity in methods. There is also evident here a desire to arrive at a better understanding of phylogeny and classification. The speaker, however, wishes to lay emphasis on another cause of confusion, namely the lack of uniformity in the concept of the genus and species.

Covering the part of the United States in which we are now located, there are two standard texts. Not long since I made a comparison of the scientific names in use in about one-third of one of these floras with the corresponding names in the same families in the other flora. It appeared that the names used in this flora differed in one or the other parts of the binomial, or in new names not found in the other flora to the extent of 19 per cent of the names employed in the second work. As nearly as could be determined the causes were as follows:

A. Changes in name due to change in Taxonomic status (counted).
    Due to segregation

Segregation of genera	194
Segregation of species	102
Total	296
Due to union	31
Grant total	327

B. Changes in names without change in Taxonomic status.
    Different interpretation of type (estimated).. 86
    Discovery of older names (estimated).. 44
    Operation of other rules of nomenclature (estimated)............................. 86
                                                                                  ——
        Total (counted).. 216

From this record it will be seen that many more name changes are due to changes in taxonomic status than to the operation of rules of nomenclature.

In the southern United States, there are also two standard taxonomic texts, though one of them is old and very greatly in need of revision. A study was made of the names in the newer work that would be unfamiliar to a student who had previously used the older manual. The comparison here is, of course, less satisfactory, as there has been much exploration in the south since the older flora was published. Here, as in the first study, allowances had to be made for differences in area covered by the two works. The same families were taken as in the first study. The results were as follows:

A. Changes in names due to change in Taxonomic status (counted).
    Due to segregation
        Segregation of genera... 195
        Segregation of species.. 565
                                                                                  ——
            Total... 760
    Due to union... 15
                                                                                  ——
            Grand total... 775

B. Changes in names without change in Taxonomic status.
    Different interpretation of type (estimated)..................................... 144
    Discovery of older names (estimated).. 72
    Operation of other rules of nomenclature (estimated)............................ 144
                                                                                  ——
        Total (counted).. 360

In these families, which included 2808 binomial halves in the older flora, there were 1125 unfamiliar binomial halves in the newer flora, or about 40 per cent. Allowing 10 per cent for recent explorations and newly discovered species, there is still about 30 per cent of change probably due to point of view.

No tabulation of western floras has been made, but the situation there is about the same. It is not surprising, therefore, that the student, on consulting different manuals, is bewildered. Often he is antagonized. He finds not only a great difference in names, but also genera and species of quite different limits or even familiar genera standing in separate families. There seems to be no uniformity, and can one blame him for at times doubting the scientific merits of our subject?

While taxonomy is a science, and we as workers in that field are trying to develop it as such, we must not forget that more than many other branches of knowledge it is a hand-maiden to workers in other fields. Dealing as it does with the kinds of plants, it deals with the orderly knowledge of the fundamental materials with which the forester, agronomist, horticulturist, floriculturist, geneticist, pathologist, cytologist, anatomist, and physiologist are concerned. These workers have a right to demand a certain consideration. The taxonomist,

concerned as he is with the orderly arrangement of knowledge with respect to plants, is of little use to other workers if his arrangement of knowledge is un-usable. He must serve two masters. He must develop his science and he must also have his product in such form that those depending upon it as a foundation for their work may find it a real help. The scientist is interested in new develop-ments; the general worker wants stability and simplicity in taxonomy. While the taxonomist must be ever on the alert for new discoveries in his science, he must be equally mindful of the other fellow and not make innovations before their validity is assured. New species should be proposed only when their validity is fully demonstrated. Changes in generic limits should be made with equal reluctance. The whimsical proposal of species and changes in taxonomic status, of which we have seen so much in recent years, has no justification. It gives little regard to the rights of others, reminding one of the recent coal strike and the relation of its contending parties to the public. Neither can we justify the attitude taken by some botanists that if variants or little known units are described as species botanists will be compelled to give attention and study to these forms, though many of these ill-advised species will prove invalid. Such procedure ignores the inconvenience which it will cause to other large groups of workers. Force in science does not sound quite right.

But which point of view shall we follow? The diametrically opposed points of view of the so-called "splitter" and the so-called "conservative" botanist cannot be both equally advantageous to science. If we are to gain uniformity it is necessary to determine which course is best, or whether a middle course is better. To the speaker it has always seemed, pedagogically and psychologically, that fewer units are easier to grasp than many; also fewer names are easier to hold in the mind than many. Indicated relation of units is an aid in acquiring a mental grasp of a large number of objects. Comprehensive grouping gives us all these advantages. The broadly applied generic or specific name indicates relationship, while segregated groups give us a greatly increased number of units with a corresponding loss of the indicated relationship. To be sure, it is generally said by the "splitter" that the smaller groups represent more easily discerned units. Though this may sometimes be true of genera, it is rarely true of the segregated species. Even if generic segregation sometimes results in more easily discernible groups, this advantage very doubtfully offsets, for the teacher and general user, the advantages of fewer large units.

We must admit, however, that from the point of view of science the smaller units do have a value also. The geneticists have found that in many cases it is the minute unit, too indistinguishable from the mass to be of practical value that behaves as should a real unit; and the plant geographer often finds that minor and difficultly distinguishable units have definite geographic ranges, peculiar soil requirements, and interesting histories.

How then can taxonomy serve its two masters? How can it serve the general public, and at the same time the geneticist, the plant geographer and the taxon-omist? In my opinion it must, among other things, work toward uniformity of practice both in group limits and in nomenclature, reduction in number and

simplification of groups, and the maintenance of stability; and then it must recognize also the geneticists' and geographers' minor units,—but not as species. It would seem to me practical to retain the more easily recognizable, broader species, while at the same time designating the minor units as subspecies, varieties, forms, or what not, as may seem proper. Under the comprehensive species a key or synopsis could be given to show the relation of the minor units to one another. By this method the number of specific names is not increased and the practical man, the teacher, and the amateur do not need to deal with the finer divisions of the species. The proposition is not new. Many old-world authors have used it; but they have not always been practical, as generally an attempt has been made to show the relationship of the smaller units by a complicated and burdensome nomenclature. In connection with this method, however, it is not practical to show relationship by nomenclature, but rather let the key show that. Simply list under the species the subspecies, varieties, forms, etc., with their proper prefixes. The units of the geneticist may have other designations than those customarily employed by the taxonomist. Why not?

An example may serve to make clear what is meant. Several years ago I published the results of a study of *Lactuca canadensis* L. and its forms (Rhodora **22**:9. 1920). In that paper I followed the undesirable practice of indicating relationship by nomenclature as shown by the combinations *L. canadensis* L. var. *typica* Wiegand forma *angustipes* Wiegand and *L. canadensis* L. var. *integrifolia* (Bigelow) Gray, forma *angustata* Wiegand. Obviously such names are too clumsy for oral use and too long on the written labels, and their ridicule is in a measure justifiable. According to the method here proposed as preferable, following the description of *L. canadensis* L. we would have the key given in the Rhodora article but our units would read *L. canadensis* var. *typica*, *L. canadensis* forma *angustipes*, *L. canadensis* var. *latifolia*, *L. canadensis* forma *exauriculata*, *L. canadensis* var. *integrifolia*, *L. canadensis* forma *angustata*, etc. In no case would we have more than three words, thus giving a name length which usage has shown to be practical.

Some botanists have attempted to meet the problem of the treatment of species subdivision, by the use of a key as here proposed but with the designation of the subdivision by binomials as though they were species,—the so-called major species and minor species,—but this does not seem to me practical. Under this method when we meet the names *Lactuca canadensis* and *L. integrifolia* how do we know that the latter is a subdivision of the former?

It seems a fact therefore, that although we should all be interested in bringing about a uniform and stable nomenclature we should be concerned, even more, in bringing about a more uniform and practical taxonomy.

ANTARCTICA AND PROBLEMS IN GEOGRAPHICAL DISTRIBUTION[1]

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In considering the part played by *Antarctica* as a centre of plant distribution in the past, when warmer conditions prevailed in the Southern Hemisphere and there was a well developed vegetation on the Antarctic Continent as proved by recent fossil records—it is essential to investigate the present distribution and fossil records of those plants which now are found to be peculiar to the Southern Hemisphere.

A casual study of the present distribution of certain families and genera may well lead to false conclusions, as for instance in the case of the genus *Araucaria*. Today this genus is represented in Brazil, Bolivia, Chile, Australia, New Caledonia, Norfolk Island, New Guinea and the New Hebrides, but the fossil evidence proves that it was common in the Northern Hemisphere, not only in Europe and eastern Asia, but also in North America and that it was abundant in northern Europe in the Mesozoic period.

The study of plant geography, if confined to the present distribution of plants, must of necessity be incomplete, and the data available from living plants must, when possible, be supplemented by the records of the rocks: "records," as Charles Darwin said, "which represent a short chapter of the last volume of a history imperfectly kept, and of this chapter only here and there a few lines." The Juan Fernandez fern *Thyrsopteris elegans* might from its present day isolated home be regarded as a purely Southern Hemisphere plant, were it not for the occurrence of closely allied ferns in the Jurassic rocks of Yorkshire, which indicates that, in its present state of isolation, it is a remnant of a once widespread group which migrated southwards, possibly in Cretaceous times, from the Northern Hemisphere.

Professor Seward in his Hooker lecture on "The Present and Past Distribution of Certain Ferns" (Journ. Linn. Soc. Bot. **46**: [p. 219] 1922), refers also to the Gleicheniaceae, Dipteridinae and Matonineae, the Schizeaeceae and Marattiaceae, which at the present day are all largely represented in the Southern Hemisphere, yet it is found that in Mesozoic times they were distributed in Europe, Greenland, Asia, and North America as well as in the south, so that they cannot be regarded as peculiar to the Southern Hemisphere.

General the Rt. Hon. J. C. Smuts—who is a remarkable example of that rare, if not unique, combination of a great politician and a distinguished botanist—in his presidential address to the South African Association for the Advance-

ment of Science, 1925 makes out a strong case for the derivation of the South African floras from "the ancient lands of the Southern Hemisphere" as against the generally accepted view that they have migrated southwards from the north.

He points out very properly that "the special affiliations of the tropical African flora are in the Southern Hemisphere." In this flora, as he shows, there is an element peculiar to the African continent but also "more or less closely related to the floras of India, Madagascar, Australasia, and South America."

The problem is one of great interest but of extreme difficulty and complexity and the question of importance is, as it seems to me, whether this peculiarity or southern affinity can be traced to an ancient or to a more modern epoch. In other words, did the angiospermous flora originate in the north and migrate southwards and then, when it had reached the south, evolve along special lines in lands comparatively isolated from the land masses in the north, or did certain groups of plants first appear in the Southern Hemisphere in an ancient temperate Antarctic Continent and become dispersed northwards into our present day land masses of New Zealand, Australia, South America, and South Africa? Or again, it seems possible that some groups may have originated in the highlands of central Africa, or in some lost continent in the Atlantic uniting Africa and South America as Wegener suggests,[2] and migrated both to the south and to the north.

That Darwin contemplated the possibility of a former Antarctic Continent in fairly recent geological times is shown both by his remarks in the "Origin of Species" Chapter XIII, and by a letter written to Hooker on December 30th, 1858 (More Letters I, p. 116), for with reference to former continental masses in present oceans he says "at present I greatly prefer land in the Antarctic regions, where now there is only ice and snow, but which before the glacial period might well have been clothed with vegetation." Further, in writing to A. R. Wallace in 1876 (Life and Letters III, p. 231), he expressed the opinion that "there must have existed a Tertiary Antarctic Continent from which various forms radiated to the southern extremities of our present continents." While in a letter to Hooker written in 1881 (Life and Letters III, p. 248), he says apropos of the sudden development of the higher plants "I have sometimes speculated whether there did not exist somewhere during long ages an extremely isolated continent, perhaps near the South Pole."

The discovery of Jurassic plants in Graham Land, as far south as lat. 63° 15′, by the Swedish Antarctic Expedition of 1901–03, and of Jurassic plants by the "Terra Nova" Expedition, 1910, in South Victoria Land and in Buckley Island (85° S. lat.), where, as elsewhere, *Glossopteris* was discovered, and the evidence which has been obtained from Seymour Island[3] and Graham Land by the Swedish Expedition in the finding of a Tertiary Flora on Seymour Island, including *Knightia* (now found in New Zealand), *Laurelia* (now growing in

[2] See also, Irmischer, E. Pflanzenverbreitung und Entwicklung der Kontinente. Mitt. Inst. für allgem. Botanik in Hamburg 5: 17–235. 1922.

[3] Close to the Graham Land Peninsula, see Skottsberg, Die Vegetationsverhalten des Graham Landes. Wiss. Ergeb. der Schwed. Süd polar. Exped. 1901–03, IV (Lief. 13): Stockholm, 1912 [p. 12.]

South America), *Drimys, Lomatia, Myrica, Nothofagus, Araucaria,* and several ferns, affords proof of the existence of Temperate continental conditions in the Antarctic with a well developed flora both in Jurassic and in early Tertiary times.

A study of the general configuration of the earth's surface, as Thiselton-Dyer (Darwin and Modern Science, p. 308), points out, suggests a continuous and progressive dispersal of species from the centre to the circumference that is to say southwards, and if, as I gather, many physicists and geologists consider that the general lines of our continents have not greatly altered from their present positions in the north and south directions, then the present stellate figure of the land masses radiating from a northern central land area would facilitate a southern dispersal, especially when conditions in the north became inimical to plant and animal life.

Had Darwin, Wallace, and Hooker been in possession of the facts which we owe to the researches of Cheeseman, Cockanye, Skottsberg, and others, and had they also known of the fossil evidence produced by the British and Swedish South Polar Expeditions, which has been so ably discussed by Seward, Regan, Harrison, Andersson, Dusen, and others, they would have been able to make their great contributions to the problems of the geographical distribution of plants in the Southern Hemisphere even more illuminating.

The evidence before us, both from fossil and from recent plants gives strong if not convincing proof that in early Tertiary times the Antarctic land mass was not only inhabited by a temperate or possibly sub-tropical flora, but that it was also a much larger area than it is at present. The present flora of Juan Fernandez suggests that at one time these islands formed part of the Antarctic Continent or were united to the extreme south of Chile, a view which is shared by Thering and Joly, who believe that such a connection may have existed in early Tertiary times and that Kerguelen Island was probably part of a large land mass at the same period.

It also seems likely, on geological evidence, that Antarctica extended in the Tertiary epoch towards Tasmania and Australia, and so to Asia, and towards New Zealand, and the distribution of certain present-day plants in the Australasian region lends considerable support to such an extension.

From the excellent maps published by Professor Edward W. Berry in his paper, in the American Journal of Botany for 1924, read at the "age and area" symposium at Cincinnati, it will be seen that *Baiera,* the extinct genus closely allied to *Ginkgo,* from its Tertiary record might also be claimed as of Antarctic origin but for its wide-spread occurrence in the north at an earlier period of the world's history. The palaeontogical evidence with regard to the ancient ferns *Dipteris* and *Matonia,* now confined to the Indo-Malayan region, also shows stronger evidence for a northern than for a southern origin.

The geological record is, of course, unfortunately very imperfect and very largely unexplored, so that we must be prepared to modify our views extensively in those cases which appear to afford fairly certain evidence of distribution from a Southern centre, but from the evidence available it seems probable that

such genera as *Calceolaria, Jovellana, Fuchsia, Ourisia, Pelargonium, Caltha* (*Psychrophila*), *Lilaeopsis, Gunnera, Veronica* (*Hebe*), *Pernettya, Azorella, Drapetes* and other Thymeleaceae, *Nothofagus, Eucryphia, Laurelia,* probably the Proteaceae, some of the Ericaceae, and certain grasses,[4] to mention only a few examples, may have originated in some Continental area in the Southern Hemisphere, whence their descendants spread northwards and are now found represented in New Zealand and Australia on the one hand or in South America on the other, while some may also have travelled or been transported into the South African region.

It is of course possible that in early times many of the plants from which these Southern Genera have evolved belonged to the Northern region and gradually migrated to the south and that having reached the southern regions they there, in a state of some isolation, evolved peculiar types which in their turn spread again northwards into the various portions of Southern Islands and Continents, without however crossing the Equator and reaching the Northern Hemisphere. On this view we may perhaps best regard many of the present day genera which are now only found in the Southern Hemisphere.

Gleason (Amer. Journ. Bot. **10**:[p. 187]. 1923), in his interesting paper on the evolution and geographical distribution of the genus *Vernonia,* has shown that the ancestral home of the genus—as far as it relates to the North American species—is clearly tropical South America, since the more primitive types of structure are shown in the South American species.

Vernonia with its distribution in South and North America, Africa, Australia, and India may thus be regarded as a genus which has been evolved in the Southern Hemisphere and has migrated into the northern region on the American side and also into India.

How the more peculiarly southern plants, which we know today, found their way into South Africa is a more difficult problem to solve, for it seems hardly likely in the case of some examples, *Vernonia* for instance, that the somewhat primitive African species reached that continent *via* India and Abyssinia or *vice versa.* Yet from Gleason's researches into the genus it seems clear that the primitive types are to be found in South America and that they have spread thence into North America, while again some equally primitive types of this genus occur in northern Nigeria. How can we account for the presence of these primitive Vernonias today in two widely-separated and distinct continental areas, unless perhaps on the assumption that western Africa and eastern South America were once closer together, as suggested by Wegener, or were connected

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[4] With regard to the grasses which may be regarded as belonging more particularly to the Southern Hemisphere:—*Potamophila* in Africa and Australia and *Ehrharta* in South Africa and its counter parts *Tetrarrhena* and *Microlaena* in Australia and New Zealand may be regarded as genera which have evolved or developed in the South African region (Stapf, Die Gliederung der Gräserflora von Südafrika. Festschr. für P. Ascherson, Art. XXXIV, p. 391) while of more peculiarly Antarctic genera *Cortaderia* in South America and the allied "*Arundo*" *conspicua,* which occurs in New Zealand may be cited. In a very general way it may be said that the South American species of *Poa* and *Festuca* are more nearly allied to the Australian and New Zealand species than to northern forms.

by a lost continent, either of which might explain many peculiar affinities between the floras of western Africa and eastern S. America?

The present distribution of the genus *Pelargonium* again is overwhelmingly *southern*, but there are no representatives in South America, and only four, out of the 232 species recognized by Knuth, are found outside Africa. Of these one is found in Asia Minor and three are natives of Australia, one of the latter, *P. inodorum*, being found also in New Zealand.

An explanation which would fit what we know about *Vernonia*, as it occurs to-day, or the very peculiar family Vochysiaceae, would, I feel, scarcely account for the present distribution of the genus *Pelargonium*.

Pelargonium, for instance, may have originated in the Northern Hemisphere and migrated to the south, where in its new home it has elaborated its remarkable diversities of types, leaving in its track *P. Endlicherianum* in Asia Minor and spreading as far south as Australia and New Zealand.

The Tropaeolaceae of South America, which from their floral structure seem to come close to *Pelargonium* and are placed next to this genus in the "Genera Plantarum," might be considered to be the South American representatives of this genus of Geraniaceae.

The vegetative characters, succulence, watery juice and general habit of the species suggest, however, that the supposed relationship with *Pelargonium* may be apparent rather than real, and that here we may have a case of analogy or parallel development as regards floral structure, and that the genera *Tropaeolum* and *Pelargonium* are not very closely related and may have arisen from quite unrelated ancestors. If this suggestion should be correct then it would seem, on present evidence, that *Tropaeolum* is a genus which has evolved in South America and has not succeeded in spreading beyond the limits of this Southern Continent. Similar cases of parallel floral development may be cited in the Papilionaceous type of flower of such unrelated plants as *Pelargonium rapaceum* (Geraniaceae), *Schizanthus* (*Solanaceae*), and *Collinsia* (Scrophulariaceae).

Vernonia on the other hand appears, on the present day evidence, to belong to the south and from the primitive species, which possibly reached South America, Africa and India,—with only one species in Australia,—from Antarctica, the numerous modern species have been evolved.

Such a distribution is somewhat paralleled by that of *Strychnos* and one would welcome a careful revision by a competent authority of the whole of such genera as *Strychnos* and *Vernonia* from all parts of the world, in order to study not only the interrelationships of the species and possible primitive forms, but also to see whether any evidence of parallel development or parallel evolution can be discovered in the two widely-separated areas, which may have led to the production of forms closely similar to one another on general grounds, but which on close examination show that the resemblances are apparent or analogous rather than truly homologous.

In a short paper dealing with Antarctic problems it is not possible to do more than refer to a few special families and genera which appear to be typical

of the Southern Hemisphere, and to consider them as far as may be possible in the light of the fossil evidence.

The Proteaceae, which are found today in Australia, South Africa, and South America, and also fossil in Seymour Island, are certainly typically southern and it is still doubtful whether the family ever occurred in the Northern Hemisphere. Fruits, which have been referred to *Hakea* and *Orites* by Mrs. Clement Reid and Miss Chandler, have been found in the Pliocene of Holland and the upper Eocene of Hampshire, England; and leaf specimens, which have been referred in turn to *Banksia*, *Drydandra* or to *Myrica*, have been found in the Bembridge beds in the Isle of Wight. These latter were found with undoubtedly aquatic plants, as Mrs. Clement Reid informs me, and it seems that the evidence from these leaf impressions is not on very secure ground. The evidence from the fruits too is none too certain, so that for the present I do not think a possible northern origin for the Proteaceae has very strong support. The genus *Eucalyptus*, which is also typically southern, may I think be regarded as a product of the Southern Hemisphere since the fossil records in the north are, I understand, not very convincing, and Mrs. Clement Reid informs me she has never found any fossil remains of this genus or of any of the Myrtaceae.[5]

With regard to the genus *Nothofagus*, which occurs living in South America, New Zealand, Tasmania, and eastern Australia; this is generally considered to be a typical Subantarctic genus, since it has also been found fossil in the Tertiary rocks of Seymour Island. It may, of course, have once been a wide-spread genus with representatives in the Northern Hemisphere, for Miss Bandulska (Journ. Linn. Soc. Bot. **46**: p. 427. 1924), in her critical study of the cuticles of some recent and fossil Fagaceae, refers to the occurrence of the fossil *Dicotylophyllum Stopesae* Bandulska in the Eocene of Bournemouth, which she considers, from the peculiarity of its cuticular structure should be referred to the genus *Nothofagus*. If this be a correct assignation it is then a matter for consideration whether the present-day species are the remnants of a truly southern genus, which originated in Antarctica and spread northwards, or whether the genus was once widespread and is now only represented in the south. At present I think the evidence is in favor of the former hypothesis.

It is instructive in connection with the distribution of *Nothofagus* to examine that of the allied genera *Fagus*—Europe, Asia Minor, and Eastern America—

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[5] See Imischer. Mitt. Inst. für allgem. Bot. in Hamburg, **5**: [p. 147] 1922. He also gives a map (Fig. Pl. 31, 11, after Berry, 1914, Fig. 8) showing the fossil and recent distribution of *Eucalyptus*. Berry's map shows fossil localities in North America, Greenland, Western Europe, and Egypt.

L. Laurent (Progressus Rei Bot. **1**: 353–354) refers to records of Myrtaceae (*Eucalyptus*, *Myrica*, etc.) and leaves of Proteaceae as very doubtful and controversial. Schenk admits *Eucalyptus Geinitzii* in the Cretaceous and with doubt in the Tertiary. Certain fruits seem to prove the exsistence of this species in the Cretaceous of the Northern Hemisphere, but their existence in the Pliocene of Italy is very doubtful. The occurrence of both Myrtaceae and Proteaceae still requires more definite proof.

Zeiller, (Élém. Paléobot. p. 326. 1900) refers to Myrtaceae records in the Cretaceous and in the Tertiary in Europe and the United States. He adds,—the existence of a genus of *Eucalyptus* is positively attested by the flowers and fruits frequently found imprinted with leaves in the middle Cretaceous of central Europe as well as in the United States.

Castanopsis—Western North America, China, Himalaya and East Indies (see Berry "Tree Ancestors"), and also *Castanea*. From this it would appear that the Northern Hemisphere was the centre of evolution and distribution of the Fagaceae and that from an early migrant, a "*Proto-fagus,*" which reached the southern regions, the genus *Nothofagus* may have been evolved, and developed in the Antarctic.

The genus *Pernettya* with its distribution in Tasmania, New Zealand, Juan Fernandez, the Falkland Islands, and South and Central America, presents a similar problem in Antarctic geographical distribution comparable to that of *Nothofagus*, *Eucryphia*, *Gunnera*, *Acaena*, *Drapetes*, *Drimys*, *Wintera*, *Ourisia*, as well as to that of the primitive genus *Coriaria*, and other present day Antarctic genera. *Coriaria ruscifolia*, to mention a particular species, is native in New Zealand, New Caledonia, Chile and Western South America while *C. thymifolia* occurs both in New Zealand, N. W. South America and also in Central America, no appreciable difference being recognisable in the plants found in these widely-separated localities.

The geographical range of the family Coriariaceae is remarkable since, in addition to the two species cited, there are some ten others, one being in New Zealand and the rest in the Himalaya, China and Japan, and the Philippine Islands. Here we appear to be dealing with an ancient family, which was probably once widespread and is now represented by three peculiar species in the Southern Hemisphere, one of which, *C. ruscifolia*, shows considerable general similarity to the European and Asiatic species.

Then again the genus *Erica*, which is unknown in South America but is so characteristic a feature of the Cape flora of South Africa, may have had quite a different origin, for it seems possible from its distribution that it may have originated in the highlands of central or south central Africa and spread both northwards to Europe and southwards to the Cape. In the Cape region it appears to have found the ideal situation for development, for there have been produced a great number of remarkable species, and, with General Smuts, I think it is right to regard this genus as a particular development in this region.

The family Epacridaceae, is confined to the Australasian region extending to Java, Borneo, and New Guinea, with, however, the very interesting exceptions of the monotypic genus *Lebetanthus*, found in Patagonia and Fuegia, and *Styphelia*[6] *Tamaiameiae* (Cham.) F. Muell., and *S. Douglasii* (A. Gray) F. Muell., in Hawai (*see* Skottsberg Vascular plants from the Hawaian Islands Medd. Göteb. Bot. Träd. **2**:[p. 254] 1925–26). The occurrence of these two Epacrids in South America and Hawai can, I think, only be accounted for on the assumption that the family was evolved in the Antarctic region.

Skottsberg is, I think, incorrect in uniting the genera *Prionotes* and *Lebetanthus* (*see* Bot. Ergebnisse der Schwed. Exp. Pat. und Fuerlande 1907–09 K. Sv. Vet.-Akad. Handl. 56, No.–5, p. 284) as they are quite distinct genera in the

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[6] The genera *Cyathodes*, *Leucopogon*, *Astroloma*, etc. have been placed in *Styphelia* by some botanists and species of *Leucopogon* also occur in Fiji and New Caledonia, so that the family has a general Polynesian distribution.

Epacridaceae and should not be placed in Ericaceae. Mr. Hutchinson has carefully examined the specimens and finds the following characters:—

"*Prionotes*: Bracts very small and few, quite distinct from the calyx lobes; ovules numerous (30 or more) in a cluster in the middle of each cell. Flowers large. Seeds numerous. Tasmania.

Lebetanthus: Bracts numerous, gradually passing into and exactly similar to the calyx lobes; ovules 5 or 6 on a stalked placenta from near the apex of the cell. Flowers small. Seeds very few. South America.

I should retain both genera in *Epacridaceae*. The anthers are typical of that family, 1-celled and opening by a single slit but with a membranous partition down the middle .

Skottsberg's statement that the anthers of *Prionotes* opens by basal pores is not correct. He has evidently seen the picture of *Lebetanthus* in Engler and Prantl. (copied from an old drawing by Jacquinot), which shows the anthers thus. I have examined them from a very young state and find the opening is by an ordinary slit.

On account of the *hypogynous* stamens these two genera show intermediate characters between Ericaceae and Epacridacea and it is very interesting that we should have them in the Southern Hemisphere. But the balance of characters puts them in Epacridaceae.

Turning now to a few other Southern Hemisphere plants I feel I am only traversing ground which has been so fully worked over by Sir Joseph Hooker, Cockayne, Cheeseman, Skottsberg, Campbell, and others and that I can add very little to what has been said in Hooker's masterly essays on the floras of New Zealand and Tasmania.

The genus *Caltha* (*Psychrophila*), in the Southern Hemisphere is as I have shewn (Ann. Bot. **32**: [p. 421]) quite distinct from the northern section of the genus in the morphology of the leaves and all the southern species which are found in New Zealand, Tasmania, Australia, The Falkland Islands and throughout western South America as far north as Ecuador, exhibit the same structural peculiarities.

These southern Calthas were no doubt originally derived from a northern stock, but the peculiar southern facies of the genus must, I consider, be a purely local Antarctic development, which has spread both to New Zealand and Australia and also to South America.

Another genus *Lilaeopsis*—if it can truly be said to represent a single genus— is again, I think, one for whose development and distribution we must look to the Antarctic Continent. The species from Bass' Strait, Tasmania, (*L. Brownii* A. W. Hill), and those from the Falkland Islands (*L. macloviana* (Gandog.) A. W. Hill), South Georgia, the southern Andes and south Chile are all closely related and seem to show primitive characters. It may well be that from an Antarctic continental centre the genus has spread northwards into New Zealand and Australia on the one hand, and to the Andes of South America on the other and thence has penetrated into North America as far north as Alaska. The absence of this genus from Europe, Asia, and Africa, lends additional support to this suggestion.

With regard to the genera *Fuchsia* and *Jovellana* Ruiz and Pav., which is now regarded as a genus distinct from *Calceolaria*, I also feel on somewhat safe ground in submitting that they should be considered as typical developments in the Southern Hemisphere. What their ancestors may have been or

whence came they, is a matter on which I am unable to enter into here, but the occurrence of two species of *Jovellana*, *J. Sinclairii* and *J. repens* in New Zealand, so strikingly similar to *J. violacea* and *J. punctata* in South Chile, is a fact difficult of explanation on any other grounds than that this peculiar little genus had its origin in a former Antarctic land mass and was distributed in the past both to New Zealand and to South America.

The closely allied genus *Calceolaria*, which extends from the Falkland Islands and Tierra del Fuego along the Andes to Mexico, may also, I think, be regarded as a genus which has evolved entirely in the Southern Hemisphere. The geographical distribution of *Fuchsia* also closely resembles that of *Calceolaria*, *Jovellana* and *Ourisia*. In New Zealand there are three distinct species *Fuchsia excorticata*, *F. Colensoi*, *F. procumbens*, the latter being apetalous, and in this respect unlike any other species, whilst the great development of the genus (some 60 species), has taken place in the continental area of South America extending into Mexico. There seems strong reason for considering that the present day Fuchsias may be regarded as having evolved from a common Antarctic stock and that in the New Zeland region there was not that possibility for the evolution of species which was afforded by the long Andean chain in South America; thus in New Zealand we find only three representatives, which differ rather markedly in their general morphological characters from their South American relatives.

In conclusion I may remind you that some 68 genera and 89 species of plants are common to New Zealand and South America, some being found also in the Falkland Islands and in Juan Fernandez, most of which are peculiar to this Antarctic region (*see* Hooker's "New Zealand Flora" and Campbell, Amer. Journ. Bot. **10**:[p. 532], 1923).

In addition to the identical species, such for example as *Sophora* (*Edwardsia*) *tetraptera*, *Veronica elliptica*, and others already mentioned, there are some very interesting and instructive examples of "representative" genera and species as Hooker pointed out, in the now widely separated regions of New Zealand and South America.

Knightia for instance, a New Zealand genus which is found fossil on Seymour Island, is represented by the genera *Embothrium* and *Lomatia* in South America, the latter being also found fossil in Antarctica and living in Australia and Tasmania. The typical South American genus *Escallonia* is represented in New Zealand by *Carpodetus*, while *Drimys* and *Wintera*, to cite another example, are represented by *Wintera* (*Drimys*) *axillaris* in New Zealand, *Drimys antarctica*, fossil in Seymour Island, and *D. Winteri* in Chile and Juan Fernandez, while this southern genus *Drimys* also extends both to Central America and to the mountains of Borneo.

It may be almost impossible in these latter days to make any certain pronouncement as to which natural families or genera, if any, actually originated in the Southern Hemisphere, when it is remembered that there have been a succession of alternations of warm temperate and cold glacial periods at various geological epochs not only in the Arctic but also in the Antarctic regions. It

seems reasonable, however, to believe that with the occurrence of cold periods in the north there must have been an extensive migration of plants towards and probably across the Equator, and conversely, with the oncoming of Antarctic glacial periods, southern plants would have traveled northwards through the Australian region to Malaya and beyond the Andes of South America to Central America, possibly also there would have been a migration to South Africa.

Whether independent evolutions of families or genera occurred both in the Northern and Southern Hemispheres can now only be a matter of conjecture. There is, however, I think some evidence in support of the view that certain groups may have arisen in a former Antarctic Continent, and possibly also in a lost continental area, which may have linked Western Africa and Eastern Brazil, and which may have been the birthplace of certain genera (*Elaeis*, *Vernonia*, etc.), now found both in West Africa and in South America. Again, as I have already pointed out, it seems highly probable that certain northern genera which apparently migrated to the Southern Hemisphere, perhaps in Cretaceous times, there evolved independently and produced genera and species which are now regarded as peculiar to that Hemisphere.

That there was a large and extensive land mass, which we may call Antarctica seems certain, from the evidence afforded by a study of the living and fossil floras, and it seems equally certain that from this lost continent, which enjoyed from time to time a temperate or even a subtropical climate, plants were distributed to South America on the one hand and to Australia and New Zealand on the other, either by means of direct land connections or by means of a chain of Islands.[7]

[7] Prof. L. Harrison in "The American Naturalist" (60: [No. 669 July-August, p. 374] 1926) brings forward some interesting evidence for 'Antarctic radiation' on faunistic grounds derived mainly from his studies of the crayfishes and their temnocephaloid parasites which are peculiar to the Southern Hemisphere. His evidence and conclusions go to support the evidence obtained from the study of the Southern flora that there was formerly an extensive inhabited land area, Antarctica, which at one time came into fairly close relationship geographically with the southernmost points of South America, New Zealand, and Australia.

SOME RELATIONSHIPS OF THE FLORAS OF THE NORTHERN HEMISPHERE[1]

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The earliest botanists in North America, seeing in the more conspicuous plants about them resemblances to those they had known in Europe, had a natural tendency to look upon them as belonging to the same species. Thus, our Red Cedar, *Juniperus virginiana* L., long after Linnaeus had pointed out the difference, continued to pass as *J. Sabina* L., and it is only within a couple of decades that the trailing shrub of boreal America, *J. horizontalis* Moench, has been generally recognized in America as specifically different from the Old World Savin.

Our Eel Grass of fresh waters, *Vallisneria americana* Michx., distinguished at once from the plant of southern Europe by its coarser habit and by the very large acuminate staminate spathes on short and thick peduncles, still appears in our American manuals as the European *V. spiralis* L., notwithstanding the fact that the more delicate European plant has the staminate spathe much smaller, blunter and on elongate filiform penduncles.[2] As a general rule it may be asserted that species, like *Vallisneria americana* (map 1), which in America are confined chiefly to the Alleghenian region, will be found to differ in very fundamental characters from their nearest allies of continental Europe.

The illustrations of this general principle are legion but three cases besides *Vallisneria* and *Juniperus virginiana* must suffice. The little *Anemone* of open woods and thickets in Alleghenian America, which long passed as *A. nemorosa* L., has white scaly rootstocks and in achenes and other technical characters is quickly separated as *A. quinquefolia* L., the European *A. nemorosa* being a plant with stouter, darker and straighter, hardly scaly rootstock. The European Wood Sorrel, *Oxalis Acetosella* L., has narrowly obovate, scarcely notched petals and the ovoid capsules are longer than broad; the plant of the eastern American forest, which regularly passes as identical with the European, has oblong, deeply notched petals and the capsules oblate, broader than long. It is really *O. montana* Raf.[3] In American manuals we recognize two species of *Hepatica*, one called *H. triloba* Gilib., the other *H. acutiloba* DC.; the latter endemic, the former long looked upon as identical with the European species.

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 19, 1926.

[2] For detailed discussion see Fernald, The diagnostic character of Vallisneria americana. Rhodora **20**: 108–110. 1918.

[3] For detailed discussion see Fernald, The validity of Oxalis americana. Rhodora **20**: 76–78. 1918; and a second note, Oxalis montana. Rhodora **22**: 143, 144. 1920.
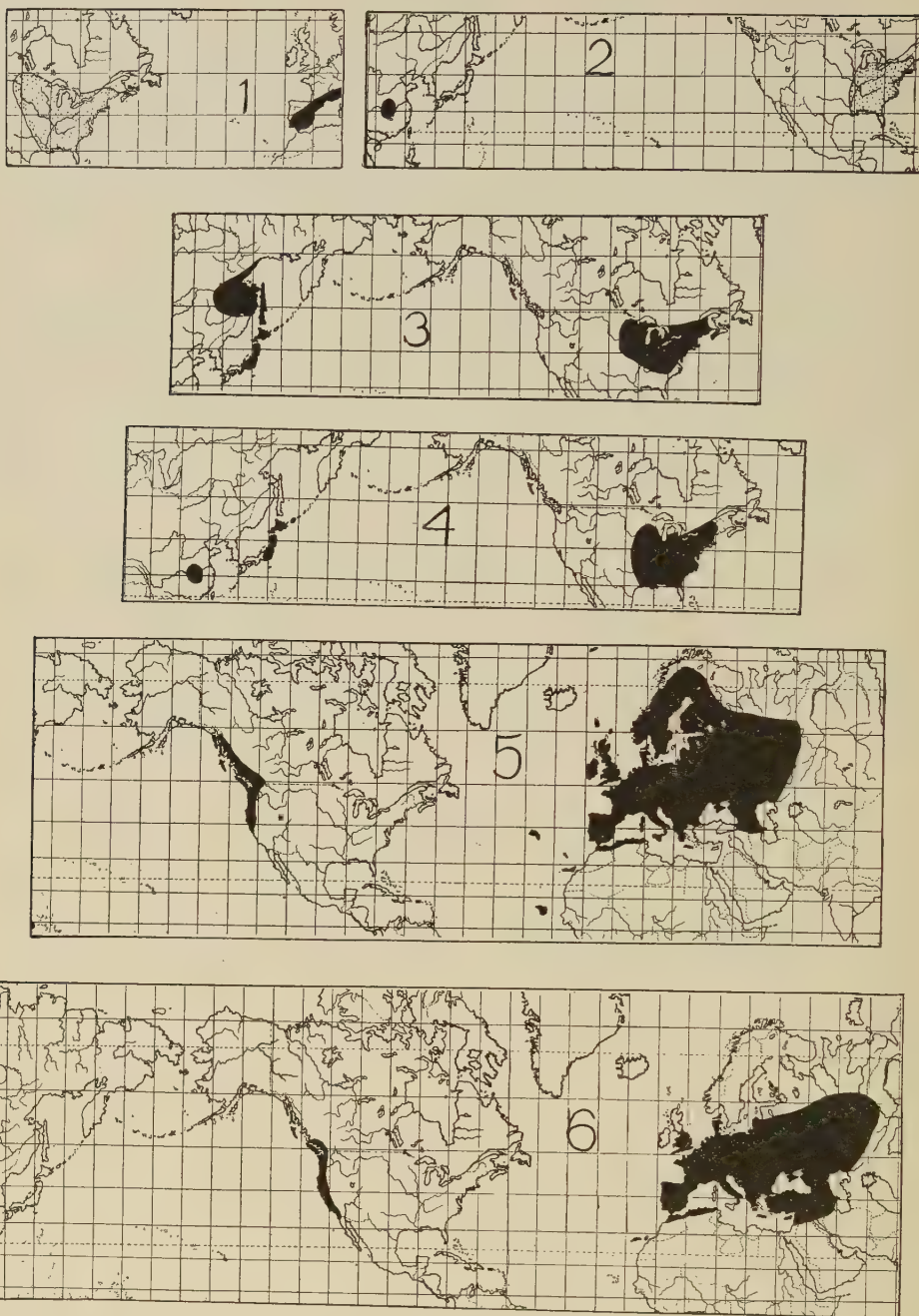
MAPS 1–6. Ranges of, 1, *Vallisneria spiralis* (European) and *V. americana* (American); 2, *Liriodendron Tulipifera* (American) and *L. chinense* (Chinese); 3, *Symplocarpus foetidus;* 4, *Polygonum virginianum;* 5, *Blechnum Spicant;* 6, *Equisetum maximum.*

H. triloba (or better *H. nobilis* Schreb.) is truly European, a plant with sessile, ovoid, short-beaked achenes; but in both the American plants the achenes are fusiform, distinctly stipitate, and slenderly beaked. Neither of these plants is like the European; and the species which in America erroneously passes as *H. triloba* is really *H. americana* (DC.) Ker.[4]

These plants, to which should be added such pairs as *Luzula pilosa* (L.) Willd. and *L. saltuensis* Fern., *Maianthemum bifolium* (L.) DC. and *M. canadense* Desf., *Ranunculus Flammula* L. and *R. laxicaulis* (T. & G.) Darby, as well as *Scrophularia nodosa* L., and *S. marilandica* L., are obviously related though perfectly distinct species and it is clear that they have long been geographically isolated. The American species of these pairs occur with or in the general region of *Liriodendron* (map 2), *Thuja*, *Comptonia*, *Carya*, *Magnolia*, *Sassafras*, *Hamamelis* and the other genera whose ancestry is clearly traced back to the Mesozoic or early Cenozoic forests of the northern hemisphere. Such ligneous types have mostly vanished from western Eurasia but most of them now survive as isolated relics in eastern North America and eastern Asia. With them in eastern Asia and eastern America there are very many herbaceous plants, *Symplocarpus foetidus* (L.) Nutt. (map 3), *Cypripedium arietinum* R. Br., *Polygonum virginianum* L. (map 4), *P. arifolium* L., *P. scandens* L., *Saururus Podophyllum*, *Caulophyllum*, *Panax*, *Shortia*, *Phryma*, etc., which are likewise restricted to eastern America and eastern Asia. Because of their similarity of present range these herbs are interpreted as descendants of the Mesozoic and Cenozoic flora quite as definitely as are *Carya*, *Magnolia*, *Sassafras* and *Hamamelis*. Is there any reason for not treating *Hepatica americana*, *Anemone quinquefolia*, *Oxalis montana*, and *Vallisneria americana* as equally ancient? These species as a group differ from the others only in having close allies in Europe as well as in eastern Asia, but is it not possible that in Europe a few of these early Cenozoic herbaceous types may have outlived the late Tertiary and Pleistocene disturbances?

Another but quite different isolation of plants in the northern hemisphere is shown by groups, often identical species, which occur in Europe and Pacific North America but which are absent from eastern Asia and eastern America. This type of range is shown by the Hard Fern, *Blechnum Spicant* (L.) Sm. (map 5) and the Giant Horsetail, *Equisetum maximum* Lam. (map 6), both of them as characteristic of Pacific North America as of Europe; while the protean *Polypodium vulgare* L. (map 7) of Europe and western America is replaced in eastern America and in eastern Asia by the more stable species, *P. virginianum* L.[5] Just what this identity of some species of Europe and western North America to the exclusion of Asia and eastern North America means, is not clear. Obviously, the climates of Pacific America and Atlantic Eurasia are similar but it is difficult to believe that climate alone can account for such segregations, and, if these plants are relics of the wide-ranging Tertiary flora, it is most singular that the great Pliocene and early Pleistocene uplifts of western Eurasia and

[4] See Fernald, The specific characters of Hepatica americana. Rhodora **19**: 45, 46. 1917.

[5] For detailed discussion see Fernald, Polypodium virginianum and P. vulgare. Rhodora **24**: 125–142. 1922.
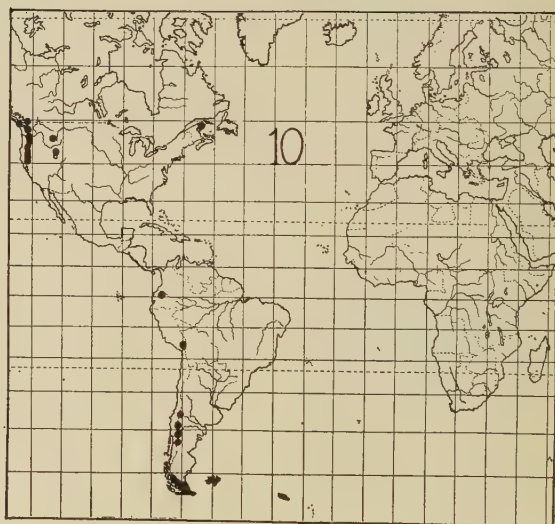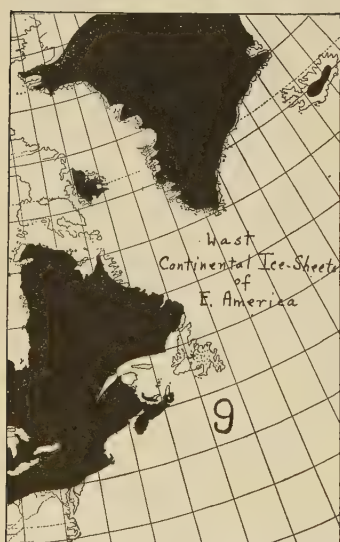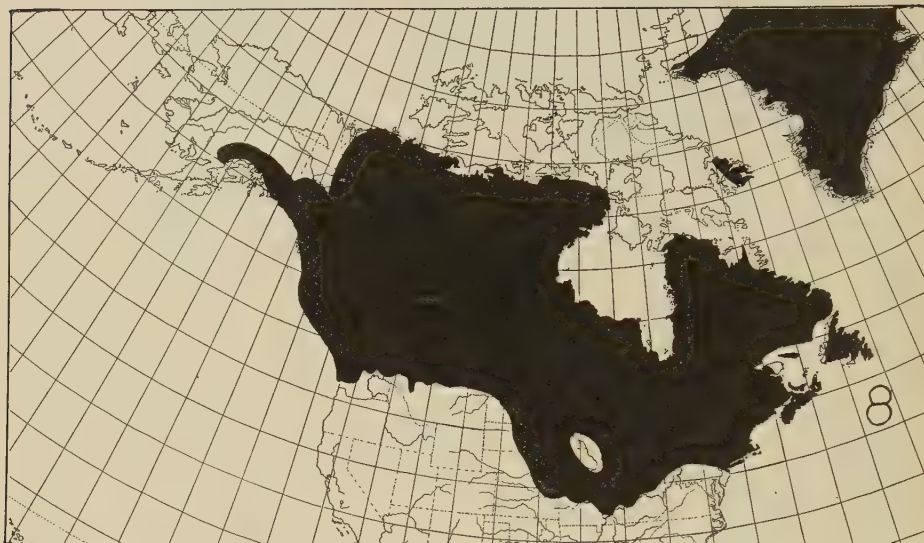
MAPS 7—10. Map 7, Ranges of *Polypodium vulgare* (black) and *P. virginianum* (dotted; 8, Maximum Extent of Pleistocene continental Glaciers in North America; 9, Extent of the latest continental Glaciers of eastern North America; 10, Range *Polystichum mohrioides* (excluding Amsterdam Island.

western America and the later Pleistocene glaciations which eradicated so many plants, especially from Europe, while leaving them in possession of eastern Eurasia and eastern North America, should have reversed the results in these cases.

But my special aim is to call attention to certain areas of northern and eastern America and of Europe which, lying near or north of the southern limits of the continental ice-sheets of the Pleistocene, have retained some peculiar relics of a flora which apparently was widespread in mid-Pleistocene time but which already shows obvious signs of senility and of relic-endemism.

In North America the earlier advances of Pleistocene continental ice-sheets were probably much more extensive than the latest or Wisconsin glaciation. As yet our knowledge[6] of the limits of the different advances is very incomplete but we have proceeded far enough to recognize that the Arctic Archipelago, most of Alaska, the Torngat Mts. of northern Labrador, and considerable areas about the Gulf of St. Lawrence were not crossed by the continental ice-sheets or at most had only trivial and very local extensions from them; while the region south of the Arctic continental coast, extending from central Labrador, western Gaspé, New Brunswick and Nova Scotia west across the Canadian plains was vigorously scoured (map 8). Very recently indeed it has been shown[7] that, although Newfoundland as a whole was thinly covered by continental ice during earliest Pleistocene time, that region, after the succeeding long interglacial epoch of hundreds of thousands of years, had only local and unimportant glaciation in the last or Wisconsin advance. The topography, resulting from hundreds of thousands of years of undisturbed weathering, shows high talus-slopes, sharp crests and deep mantles of angular gravel *in situ*, features which in the areas of most recent continental glaciation are completely obliterated. In eastern North America the last or Wisconsin glaciation, ending probably 25,000 to 30,000 years ago, extended south to Nova Scotia, southern New England, Long Island, New Jersey, Pennsylvania, and the Ohio Valley, but within these latitudes, to summarize the preceding statements, the areas in which the Wisconsin glaciation was largely ineffective in removing the accumulated rock-debris and in rounding off the sharp crests was centralized about the Gulf of St. Lawrence (Gaspé, the Magdalen Islands, Newfoundland, Anticosti and the Mingan Islands, and the southeastern corner of Labrador) and the Torngat region of northern Labrador (map 9).

As I have recently shown,[8] these areas which have been free from vigorously eroding continental ice-sheets since the opening of the long interglacial epoch (preceding the last continental advance) are at once distinguished by the presence of hundreds of species which in eastern America are known nowhere else—and which are interpreted as relics of the flora which was widespread across the boreal regions during the long interglacial epoch but which was recently

[6] For summary see Fernald, Persistence of plants in unglaciated areas of boreal America (Mem. Gray Herb. ii), Wem. Am. Acad. 15 (3): 1925. Since this paper was read two authoritative books upon the subject have appeared; Coleman, A. P. Ice ages (especially Part I). New York, 1926; and Anteve, Ernst. The last glaciation. Am. Geogr. Soc. Res. Ser . No.17. 1928.

[7] Coleman, A. P. The Pleistocene of Newfoundland. Journ. of Geol. 34: 193–223. 1926.

[8] Fernald, Persistence of plants in unglaciated areas of boreal America, l.c.

exterminated from the intermediate areas by the advance of the Wisconsin ice-sheet. Such isolations in the regions uninvaded by the latest continental ice are indicated by *Polystichum mohrioides* (Bory) Presl (map 10), *Senecio resedi-*
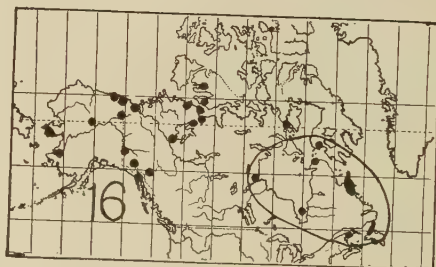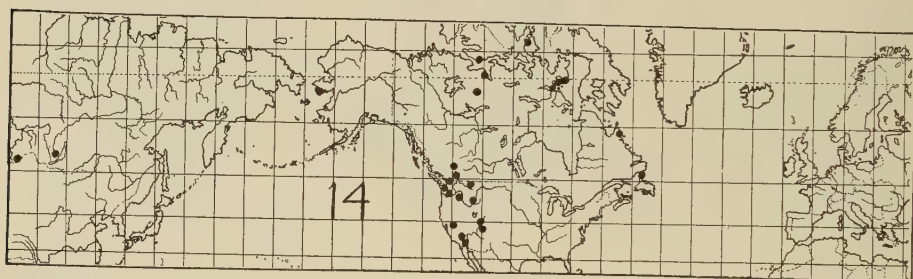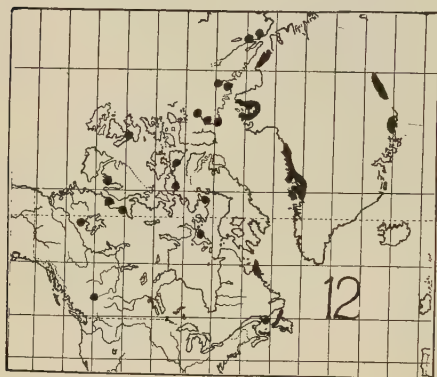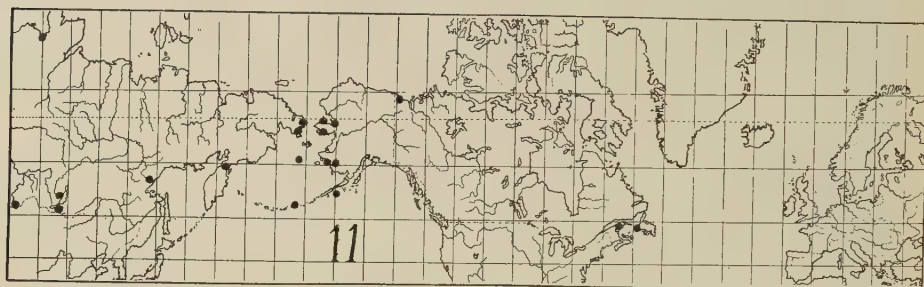
Maps 11–16. Range of, 11, *Senecio resedifolius;* 12, *Lesquerella arctica;* 13, *Erigeron compositus;* 14, *Crepis nana;* 15, *Oxytropis arctobia;* 16, *Salix Richardsonii* and (in ellipse) *S. calcicola.*

folius Less. (map 11), *Lesquerella arctica* (Wormskj.) Wats. (map 12), *Erigeron compositus* Pursh (map 13) and *Crepis nana* Richardson (map 14); and restriction to unglaciated arctic America by *Oxytropis arctobia* Bunge (map 15). With these plants, chiefly of western America, now isolated on the unglaciated areas about the Gulf of St. Lawrence or in northern Labrador there are many endemics (more than 100 known in this as yet scarcely explored area) which are closely related to species of remote geographic range, rather than to species of the adjacent continental region. Such endemics are well illustrated by *Salix calcicola* Fern. and Wieg. (map 16), eastern representative of the northwestern *S. Richardsonii* Hook.

These hundreds of endemic or nearly endemic (epibiotic)[9] species are so closely confined to the spots which were uninvaded by the last continental ice that in the 25,000 to 30,000 years since the ice-front of this glaciation began to melt, they have shown no strong tendency to extend their ranges into the closely adjacent and recently deglaciated areas, even where lithological conditions are essentially identical. Thus, in Newfoundland, where the Wisconsin ice seems to have had its greatest development in mountain-ravines and near the central and southeastern sections of the island, the plants of the unglaciated or only anciently glaciated western area remain localized in that area; and in Gaspé and northern Labrador they show a parallel restriction to the unglaciated spots. Such evidence indicates that this flora was aggressive and made a rapid spread about the boreal regions of America in the long interglacial epoch preceding the Wisconsin glaciation; but that it now consists of already waning types, too old or too conservative to spread into closely adjacent and virgin soils.

In Europe a perfectly parallel situation is found. The extent[10] of continental glaciation there is indicated in map 17. The signs of the first glaciation were mostly obliterated by the second and most extensive continental sheet, which covered Iceland and Ireland and all but southernmost England and eastward reaching the Ural. The third sheet left southern Ireland and most of England undisturbed and eastward merely crossed the White Sea. After a very protracted interglacial epoch, the last or Great Baltic Glacier, nearly synchronous with our Wisconsin sheet, failed to invade the northern borders of Norway and the Kola Peninsula or the region eastward; and southward it left western Denmark and the area to the west, including the Faroë Islands almost untouched, and invaded only a portion of Iceland.

In other words, since the beginning of the long interglacial epoch which preceded the latest continental ice-sheets of North America and of Europe, the following regions have had only local glaciation or have remained unglaciated: western North America including most of Alaska, the Arctic Archipelago, northwestern Greenland and many nunatacks along the coast of Greenland, northern and southeastern Labrador, and the region from Newfoundland to

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[9] "Species which are the survivals of a lost flora—for these I propose the name *Epibiotics*, which signifies survivors."—Ridley, H. N. Journ. Bot. **63**: 182. 1925.

[10] Map 17 is copied from Fig. 3 of Osborn and Reeds, Old and new standards of pleistocene division in relation to the prehistory of man in Europe. Bull. Geol. Soc. Am. **33**: 411–490. 1922

northern Cape Breton and Gaspé; much of Iceland, the Faroë Islands, the British Isles, much of Denmark and the region southward, and the Arctic border of Europe. It is, therefore, significant that at least 100 species which in America are restricted to or which center upon the areas uninvaded by the last continental ice-sheet should occur in Europe, likewise, only in the areas which were there not covered by the Great Baltic Glacier or should very definitely have their centers of distribution at these points. This considerable flora, which, in Europe as well as in America, occurs only outside the areas which were invaded by the latest continental ice-sheets, is well illustrated by *Epilobium latifolium* L. (map 18), *Lomatogonium rotatum* (L.) Fries (map 19), *Campanula uniflora* L. (map 20) and *Eutrema Edwardsii* R. Br. (map 21). In Europe, as in America, these plants, now persisting as relics from the earlier Pleistocene flora, have rarely invaded the closely adjacent regions (in Europe the Scandinavian Alps) which were denuded by the last continental glacier and which, one would suppose, would offer most attractive habitats for them. The situation in Europe is, then, quite parallel with that in America, for in Europe, just as in America, these arctic species seem to be so ancient as to have lost their capacity for pioneering.

Another feature about these species which in Europe are restricted to the arctic and subarctic areas outside the regions invaded by the Great Baltic Glacier is most instructive. In many cases (e.g., *Antennaria alpina* (L.) Gaertn. and *Arnica alpina* Olin and Ladau) there is a single wide-ranging arctic species, usually nearly or quite circumpolar, but in more southern latitudes of America, as in western Newfoundland, Gaspé, the Torngat region of Labrador, and the Cordilleran region of western North America, they are represented by large series of highly localized and often sharply defined endemics or epibiotics. In many cases, as illustrated by *Antennaria vexillifera* Fern. and *Arnica Griscomi* Fern., the local epibiotic is known only from two very restricted areas—one on the mountains of Gaspé, the other in northwestern Newfoundland; while such species as *Antennaria Peasei* Fern. and *A. Longii* Fern. are known from but a single limited area each—the first on the Gaspé mountains, the second in northernmost Newfoundland. The extreme rarity of these plants, themselves presumably local derivatives from the circumpolar species, is taken as an indication that the local endemics of the unglaciated areas are, like the species with disrupted ranges, already too conservative to spread into the neighboring and more youthful areas.

This interpretation gathers force when the floras of the unglaciated or only anciently glaciated areas are compared with those of neighboring regions which were denuded by the Wisconsin or last advance. Peninsular southwestern Nova Scotia, for example, was scoured by ice during the Wisconsin glaciation and its flora has been derived in post-Pleistocene time, partly from the continent by way of New Brunswick, partly from the southern coastal plain by way of the formerly elevated but now submerged continental shelf (map 22). This latter element of the flora, reaching Atlantic Nova Scotia from the south at the close of Pleistocene time and consisting largely of species of New Jersey, such as

Map 17, Extent of chief Pleistocene Ice-Sheets of Northern Europe (after Reeds).

Chief Pleistocene Sheets of Northern Europe
2nd (Greatest) Advance
3rd Advance
4th (Last) Advance

17
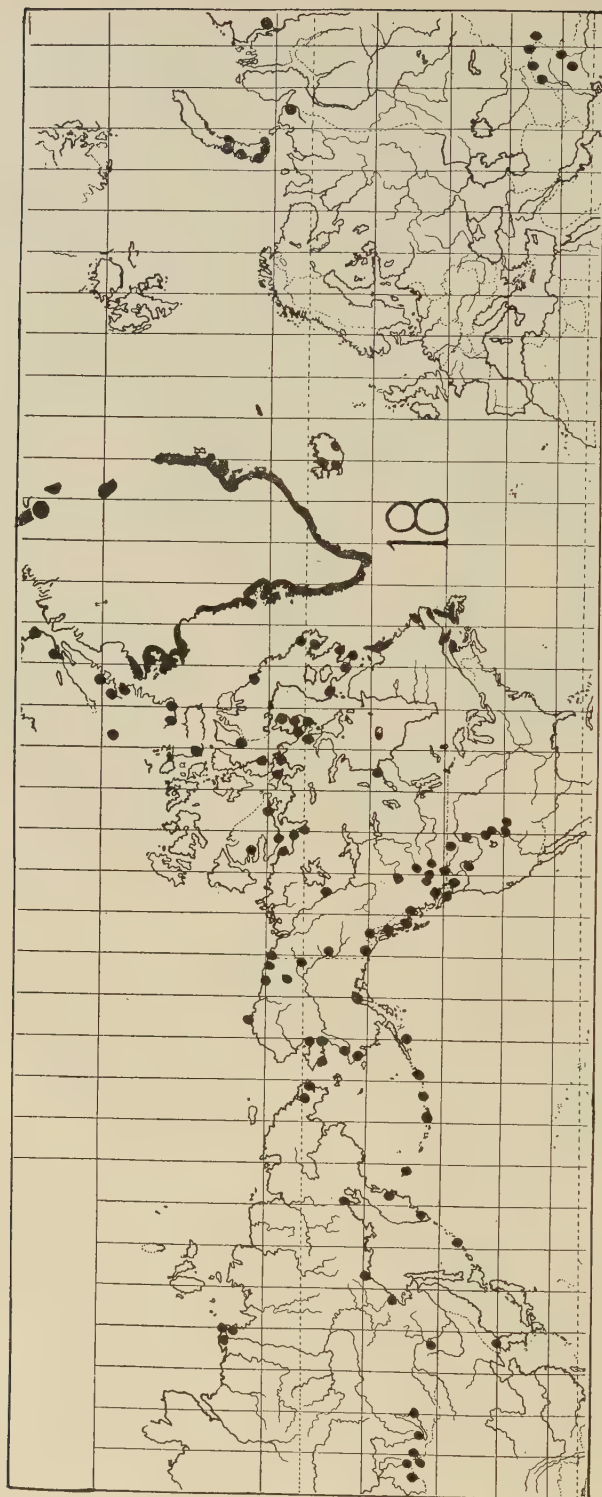
Map 18, Range of *Epilobium latifolium.*
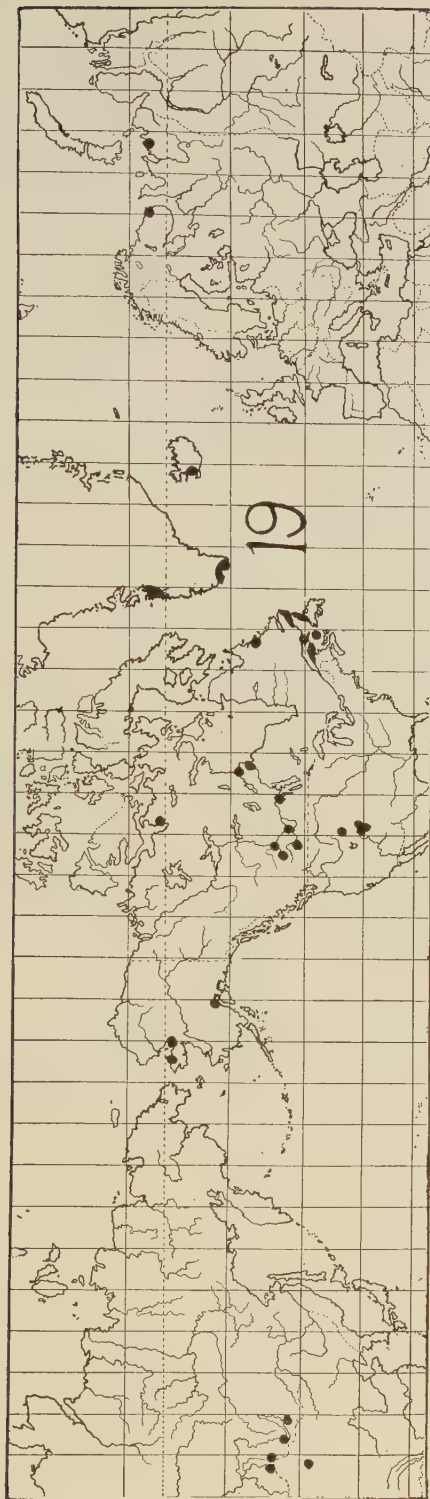
Map 19, **Range** of *Lomatogonium rotatum.*
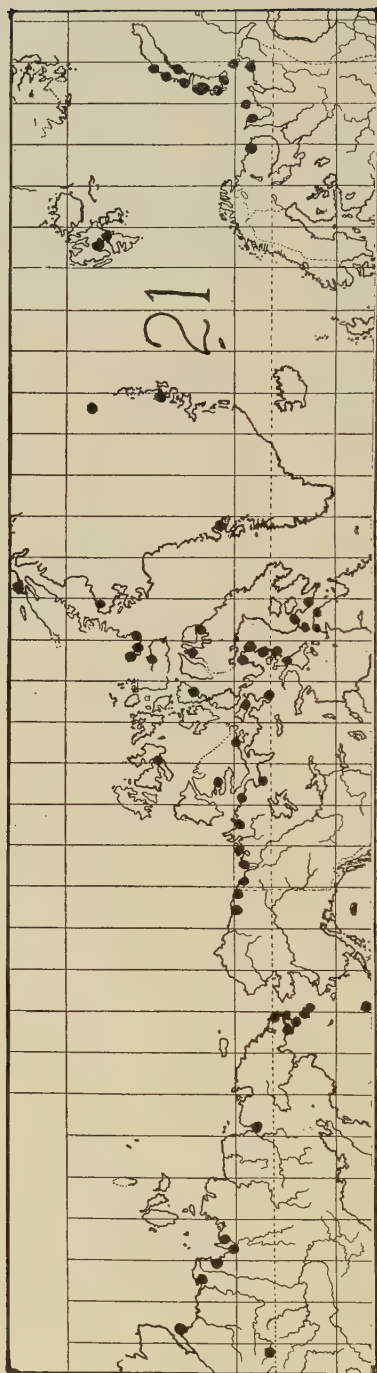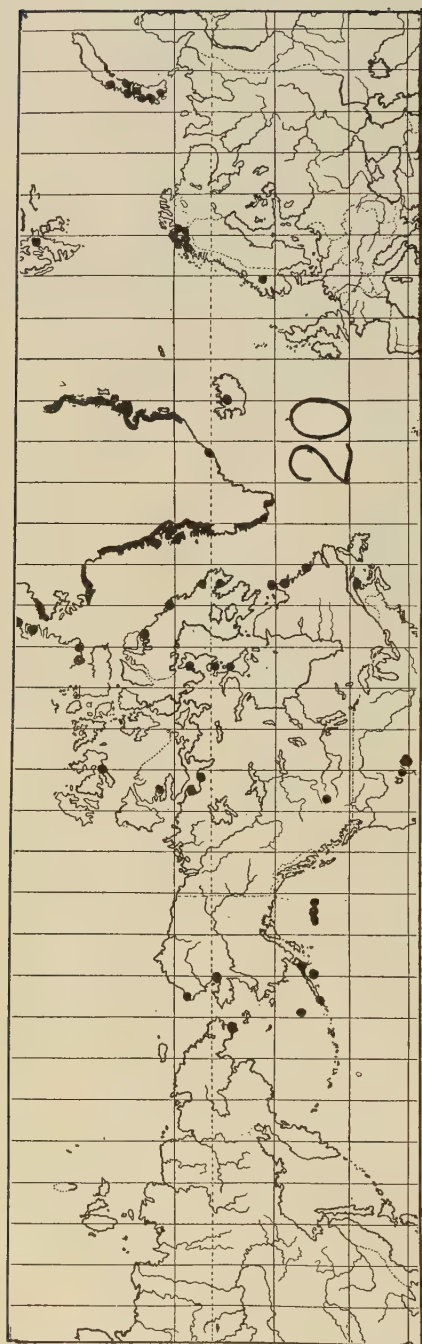
Map 20, Range of *Campanula uniflora.* Map 21, Range of *Eutrema Edwardsii.*
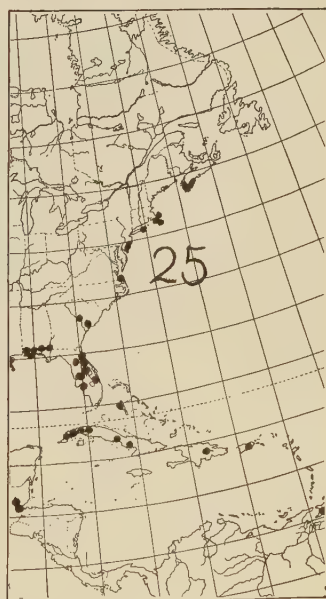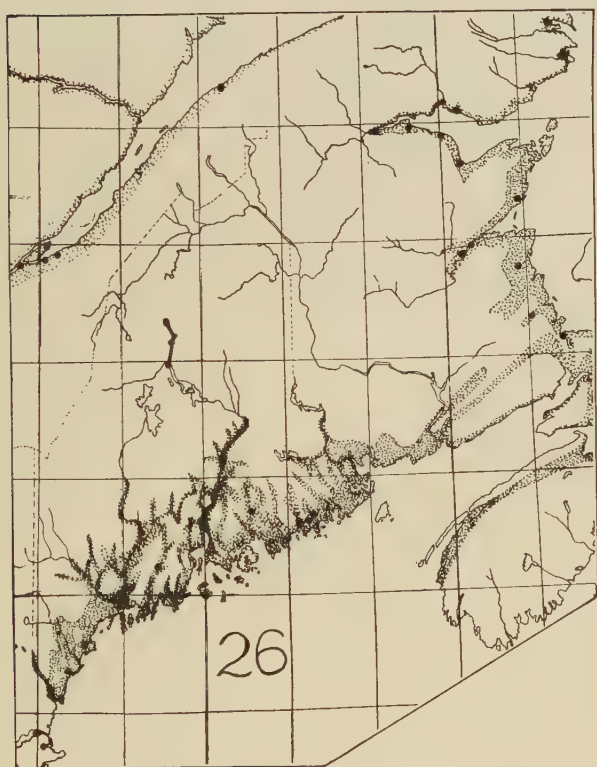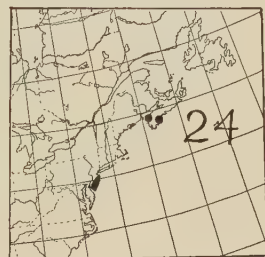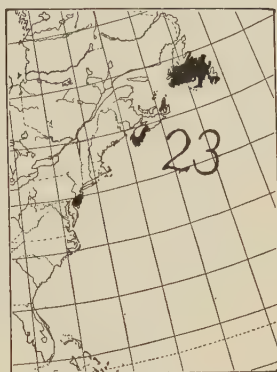
MAPS 22–26. Map 22, Submerged Continental Shelf of eastern North America; 23, Range of *Schizaea pusilla;* 24, Range of *Lophiola americana;* 25, Portion of Range of *Utricularia subulata;* 26, Portion of Champlain Subsidence and Range of *Bidens hyperborea* (omitting station at mouth of Rupert River).

Schizaea pusilla Pursh (map 23) and *Lophiola americana* (Pursh) Wood (map 24), or even of tropical America, such as *Utricularia subulata* L. (map 25), contains nearly 200 representatives in Nova Scotia; yet in this flora of the warm South, now isolated in a comparatively cold and bleak northern area, Nature, in the 25,000 to 30,000 years since the close of the Wisconsin glaciation, has set off only one endemic species, a weed-like annual, *Agalinis neoscotica* (Greene) Fern., the specific distinctness of which has been doubted by the monographer of the group. It is, of course, not improbable that this species already existed on the formerly elevated continental shelf.

Or, again, let us look at a plant restricted to the very limited belt by the margin of the sea which was submerged at the close of the Wisconsin glaciation— the marine invasion known as the Champlain Subsidence. The regions from Maine to the lower St. Lawrence thus submerged[11] are shown in map 26; and the black dots indicate the known stations for a remarkable species, *Bidens hyperborea* Greene. This species, occurring exclusively on fresh tidal mud in estuaries from eastern Massachusetts to Quebec, is distinguished from all other species of *Bidens* by its slender-based (almost stipitate) strongly corrugated achenes with a convex cartilaginous summit. Isolated, as its different colonies are, in the fresh river-mouths, with no connecting colonies around the intermediate brackish and saline shores, *Bidens hyperborea*, known only within the narrow area covered by the Champlain Sea,[12] presumably had a continuous range when the great volume of water from the melting ice-sheet freshened the shallow margin of the inner Gulf of Maine and Gulf of St. Lawrence, then almost land-locked by the elevation of the continental shelf outside; but today its colonies are positively segregated. The botanist who has closely studied them is able, from the habit and leaves of the plants and the development of the outer involucral bracts, to say whether a given specimen comes from the tidal flats of the Cathance River or the Penobscot in Maine, the Miramichi in eastern New Brunswick or the Dartmouth in Quebec; but wherever these regional variations occur they all have the unique achene which at once differentiates *B. hyperborea* from all other species. *Bidens hyperborea*, then, an apparently very modern species of a notoriously plastic genus, although occupying phenomenally segregated spots since the withdrawal of the Champlain Sea (perhaps 15,000 to 20,000 years ago) and showing regional differences of habit and foliage, has held its fundamental specific character unchanged. Like the southern types isolated for a slightly longer period in Nova Scotia, it has not had time materially to change its most deep-seated specific character. As already stated, the behavior of these plants which have occupied their isolated northern areas for 15,000 to 30,000 years is illuminating, when compared with the conditions in the flora

[11] For much of the data in regard to *Bidens hyperborea* I am indebted to Dr. Norman C. Fassett. Since this paper was presented Dr. Fassett's discussion of the subject has appeared: Fassett, N. C. The vegetation of the estuaries of northeastern North America. (See especially 93–97). Proc. Boston Soc. Nat. Hist. **39** (3): 1928. The limits of the Champlain Subsidence are taken chiefly from Chalmers, Geol. Surv. Can. Ann. Rep. N. S. 7: (map 559). 1895; and from Stone, George H. The glacial gravels of Maine and their associated deposits (plate 2). United States Geol. Surv. Mon. **34**: 1899.

[12] The original station was on the estuary of Rupert River, beyond the limits of this map.

of Gaspé and western Newfoundland, where many species have survived un-disturbed the whole of Pleistocene time. In the latter regions endemism is pronounced and it is very clear that this extreme endemism is a direct index to the antiquity of the flora.

Another series of identities is shown in many species occurring only in Europe and in Newfoundland or the region bordering the Gulf of St. Lawrence. Some-times, as in case of *Pedicularis sylvatica* L. (map 27), *Potentilla procumbens* Sibth. (map 28), *Montia rivularis* Gmel. (map 29) and *Sieglingia decumbens* (L.) Bernh. (map 30), they are plants of fresh habitats; again, as in *Polygonum acadiense* Fern. (map 31)[13] and *Atriplex maritima* E. Hallier[14] (map 32), they are maritime; again, as in the western representative of *Habenaria albida* (L.) R. Br., our *H. straminea* Fern. (map 33), although not found in continental Europe, the species shares the Faroë Islands, Iceland, the margin of Greenland and northern Newfoundland. But the significant point is, that, whether in Europe or America, these plants have their entire range or a considerable portion of it within the areas which were uninvaded by the last advances of the continental ice-sheets. This point is particularly emphasized when we examine in detail the local occurrence of such a plant as *Atriplex maritima* E. Hallier (A. *arenaria* Woods, not Nutt.) (map 32) in Denmark (map 32a), where the northern and eastern half of the country was invaded by the southwestern edge of the last or Great Baltic Glacier, and then compare its detailed occurrence in North America. In his full statement of ranges of Danish plants, which has come to hand just as this paper is being finished, Jessen[15] enumerates four stations in Denmark for the plant, three of them west of the extreme limit of the Great Baltic Glacier, the fourth to the east within the area covered by the Baltic ice-sheet. But Professor Ostenfeld assures me that the record of the last station is due to an error, while he adds from his own experience another station in the south-western part of Denmark. In America the species is known from only seven stations, all on the Gulf of St. Lawrence (map 32b); and, even though this is a littoral plant which we should expect to make a rapid spread along shore, it has held very consistently to the margin of the formerly uplifted continental shelf (map 22) outside the limits established by Chalmers[16] for Pleistocene glaciation on the western side of the Gulf of St. Lawrence.

Related in principle to these and scores of additional cases are certain species which on one side of the Atlantic or the other have shown a greater capacity to spread from the unglaciated centers. Thus, the salt-marsh *Carex norvegica* Willd. (map 34) on both coasts has followed the saline shores; *Spartina alterni-flora* Loisel. (map 35) and *S. patens* (Ait.) Muhl. (map 36), widely dispersed on the coast of eastern North America, are highly localized in Europe. *S. alterni-*

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[13] Map 31 is derived largely from a note by Ostenfeld (Botanisk Tiddskrift **34**: 254. 1916.)

[14] See Blake, S. F. An Atriplex new to North America. Rhodora 17: 83–86. 1915.

[15] Jessen, Knud. Oversigt over Karplanternes Ulbredelse i Danmark. Botanisk Tiddskrift, **39**: 137–210. (With map.) 1926.

[16] Chlamers, Robert. Report on the surface geology of eastern New Brunswick, north-western Nova Scotia and a portion of Prince Edward Island. Geol. Surv. Can. Ann. Rep. n.s. **7**: (especially map 558.) 1895.
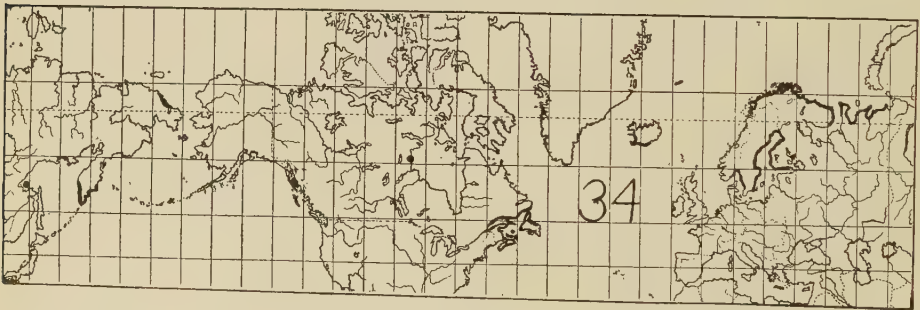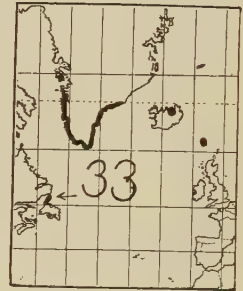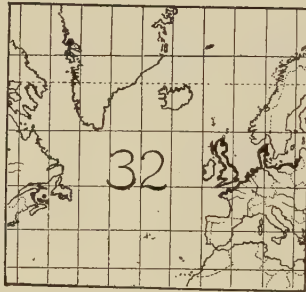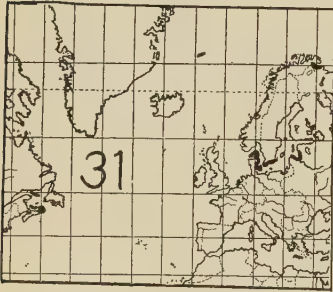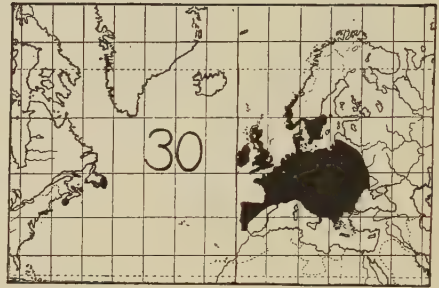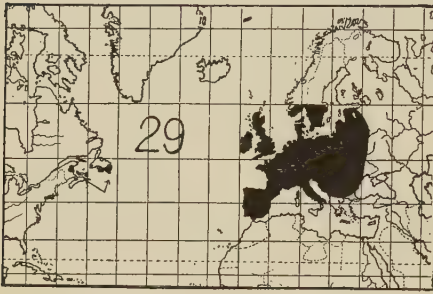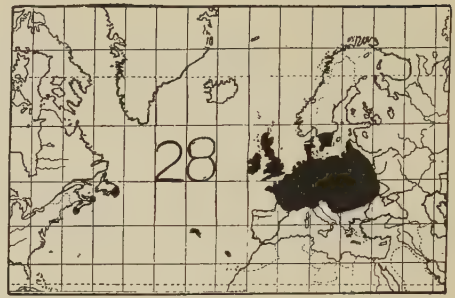
MAPS 27–34. Range of, 27, *Pedicularis sylvatica;* 28, *Potentilla procumbens;* 29, *Montia rivularis;* 30, *Sieglingia decumbens;* 31, *Polygonum acadiense;* 32, *Atriplex maritima;* 33, *Habenaria straminea;* 34, *Carex norvegica.*

flora, described from the region of Bayonne, has its second European station in southern England, south of the region invaded by Pleistocene ice. *S. patens* (including *S. juncea* Willd.) is localized on the western Mediterranean, where it has passed as the endemic *S. Duriaei* Parl. (1848) or *S. versicolor* Fabre (1850). The European specimens can be closely matched by American; and Durieu himself, who, it may be assumed, would be inclined to maintain *S. Duriaei* if he thought it a good species, treated it without reservation as identical with the American plant.[17] *Puccinellia maritima* (Huds.) Parl. (*Atropis maritima*) (map 37) is widely dispersed on the coast of Europe but is more localized in
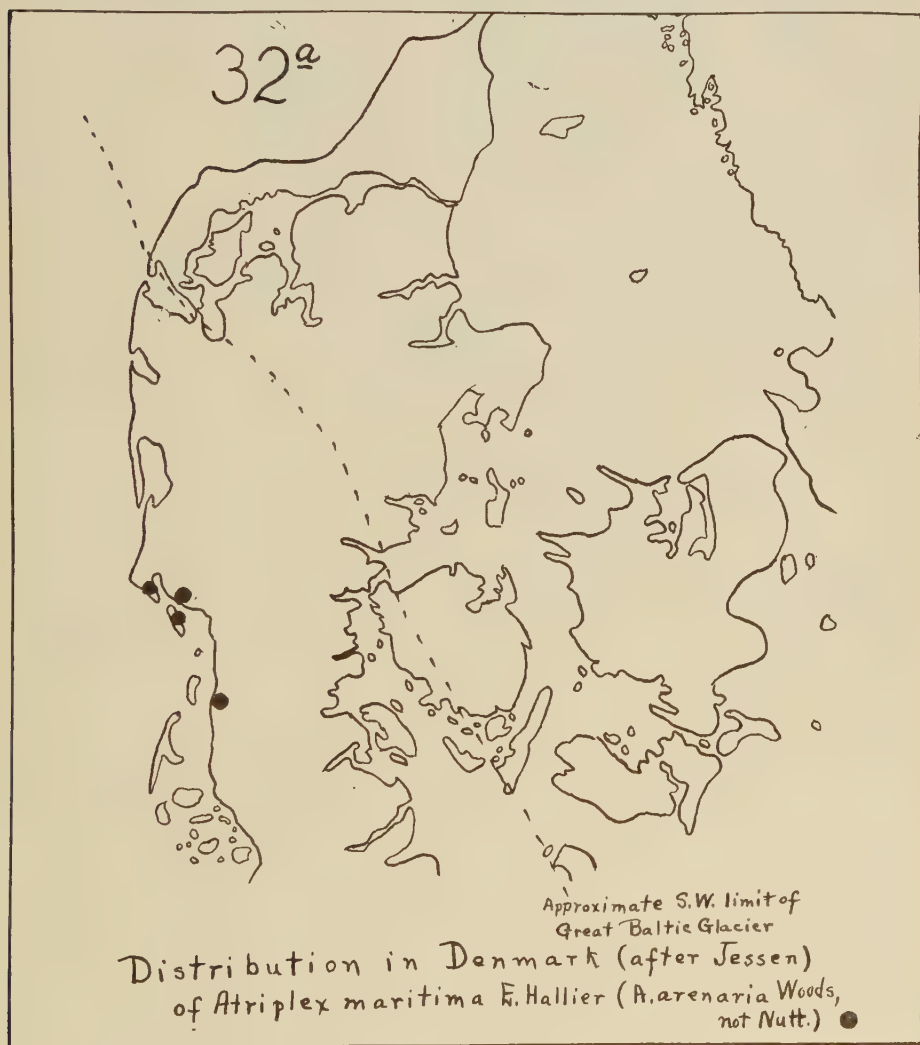
MAP 32a, Range of *Atriplex maritima*, in Denmark.

[17] See Cosson and Durieu, Expl. Sc. Alg. 2: 88. 1849. For fuller discussion of the relationships of Spartina in Europe and America see Fernald, Some notes on Spartina. Rhodora 18: 177–180. 1916.
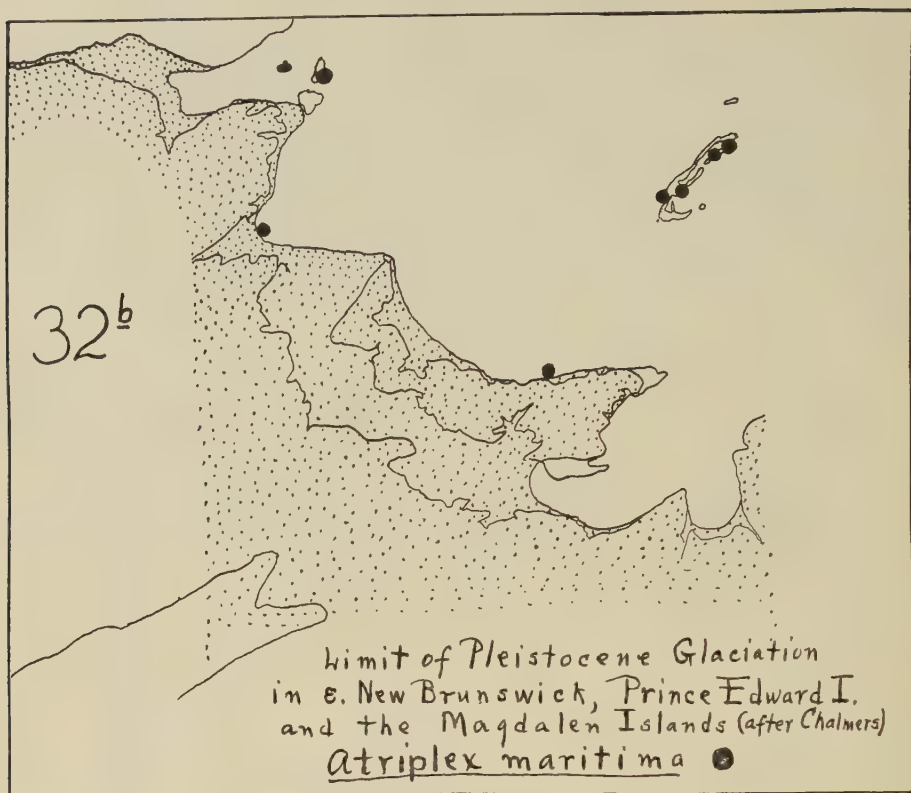
MAP 32b, Range of *Atriplex maritima* in North America.

America. Or turning to inland species, the common *Najas flexilis* (Willd.) Rostk. & Schmidt (map 38) of eastern North America, in Europe is one of the rarest of species, with about a dozen known stations[18] for living plants (in Ireland, Scotland and the Baltic countries) but with stations for fossils in recent beds in Hanover, Holstein, southwestern Norway, Sweden and East Finland. As Rendle, the monographer of the genus, aptly says, "Judging from the increasing number of localities for its fossil fruits in Northern Europe, [it] was formerly more widely spread than at present over the cooler parts of the north temperate zone."[19] Two other common North American plants have long been famous in Europe: *Spiranthes Romanzoffiana* Cham. (map 39) through its isolation in Ireland; and *Eriocaulon septangulare* With. (map 40) through its stations in Ireland and western Scotland. Many more such instances might be noted but these must suffice. The important point is, that, in these cases as in those previously discussed, the dominant American species, isolated and rare in Europe, there occurs partly if not exclusively in the regions which lay outside the last glacial advances, while the dominantly European species, localized in America,

[18] See Rendle, A. B. A systematic revision of the genus Najas. Trans. Linn. Soc.Ser. 2. **5**: 404. 1899. For further notes see Fernald, Notes on the distribution of Najas in northeastern America. Rhodora **25**: 107. 1923.

[19] Rendle, 1. c. 405.
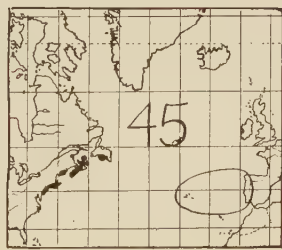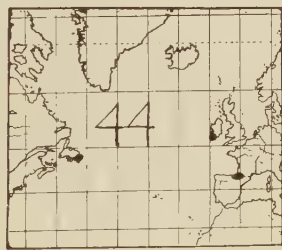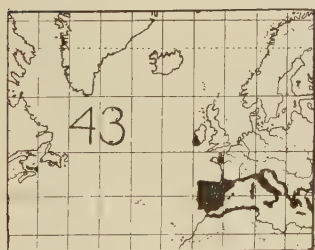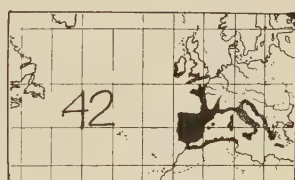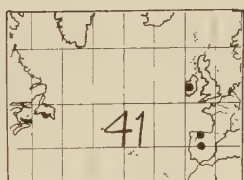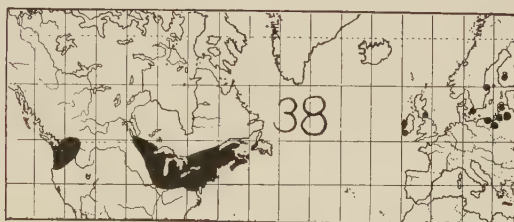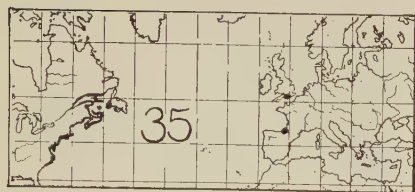
MAPS 35–44. Map of, 35, *Spartina alterniflora;* 36, *Spartina patens;* 37, *Puccinellia maritima;* 38, *Najas flexilis;* 39, *Spiranthes Romanzoffiana;* 40, *Eriocaulon septangulare;* 41, *Erica Mackaii;* 42, *Rubia peregrina;* 43, *Arbutus Unedo;* 44, *Saxifraga Geum;* 45, genus *Corema, C. alba* European, *C. Conradii* American.

have at least some of their stations in the unglaciated areas bordering the Gulf of St. Lawrence or south of the regions of continental ice.

This brings me to the last group of species to which I shall refer: the southern and Atlantic European elements,[20] a few species of which have long been famous for having rare outposts in southern England or southern Ireland. As examples I have taken five cases. *Erica Mackaii* Hook. (map 41) is very rare, restricted to the ancient Iberian region and to the section of Ireland which lay beyond the third and the fourth advances of continental ice in Europe. *Rubia peregrina* L. (map 42) is a widespread Mediterranean type, with northern areas in southernmost England, mostly south of all the continental glaciers of Europe, and in southern and western Ireland, beyond the later advances. *Arbutus Unedo* L. (map 43), a famous Mediterranean shrub, is known north of the continent only in Cork and Kerry, outside of the area of the last two continental ice-fields; and there is an unverified record of it in eastern Newfoundland,[21] in the region where *Potamogeton polygonifolius* Pourret, *Glyceria fluitans* (L.) R. Br., *Juncus bulbosus* L., *J. conglomeratus* L., *Sieglingia decumbens* (map 30), *Nardus stricta* L., *Ranunculus hederaceus* L., *Calluna vulgaris* (L.) Hull, *Pedicularis sylvatica* (map 27), *P. palustris* L., *Galium saxatile* L. and numerous other European types are clearly indigenous. · *Saxifraga Geum* L. (map 44), in Europe known only from the Pyrenees and from Kerry, was collected in Newfoundland (the exact station unknown) by Steinhauer and the specimen, preserved in Durand's herbarium at Paris, has been studied and specially noted by Dr. Britton.[22] And finally, the genus *Corema* (map 45) has but two living species, *C. alba* (L.) Don of the Lusitanian region and the Azores, and *C. Conradii* Torr., extending from Newfoundland and the Magdalen Islands to New Jersey; but a Pliocene fossil species, *C. intermedia* Reid & Reid,[23] from England and Limburg has recently been described.

In view of the facts of Pleistocene history, is it not reasonably clear that such plants as *Pedicularis sylvatica*, *Atriplex maritima*, *Spartina patens*, *Spiranthes Romanzoffiana*, *Saxifraga Geum*, *Corema*, and the many other plants of similar ranges were formerly widespread across the intercontinental region now forming the floor of the North Atlantic, or, if you prefer, that, in the long interglacial epoch preceding the last continental ice-advances in Europe and North America they made their way across the then elevated floor of the northern Atlantic; and they now persist as relics chiefly and sometimes exclusively in isolated areas from which they were not eradicated by the later continental ice-sheets and by the depression of the North Atlantic basin?

These isolations in the flora of the northern hemisphere which I have here touched upon are only a few of the interesting relationships of which we know. They are, however, sufficient, I believe, to make clear the two most important

[20] For data on these and for the European ranges indicated on maps 41–44 I am indebted to Stapf, O. A cartographic study of the southern element in the British Flora. Proc. Linn. Soc. Lond. Sess. 129: 81–92. 1917.

[21] See Fernald, Rhodora. 28: 51. 1926.

[22] Britton, N. L. Bull. Torr. Bot. Cl. 18: 270. 1891. See also Fernald, l. c.

[23] Reid, Clement and Eleanor M. Reid, A new fossil Corema. Jour. Bot. 3: 113, 114. t. 531. 1914.

needs of phytogeography: first, the active coöperation of the most accurate field-systematists throughout the world; second, the coördination of our work with that of the students of historical geology. We have much to learn from the geologist, but it is gratifying to note that, in interpreting Pleistocene and more recent phenomena, the geologist is beginning to look for cues to the field-botanist. The geologist bases his stratigraphic classification and his interpretation of geological history largely upon the paleontologist's identifications of fossil animals and plants; but, while he has always admitted the significance of the distribution of plants after they have become fossils, he has been too often disinclined to recognize that the ranges of living species are sure indices to the more recent geological changes.

This aloofness of the two sciences is being overcome. European phytogeographers, Briquet and numerous others, have had their successes in guiding to the truth the students of Pleistocene phenomena. And I may be pardoned if, by way of illustration, I refer with satisfaction to some of my own gropings in the dark on this side of the Atlantic. Fifteen years ago, finding no help from any geological reports, I first broke across the barrier and on the basis of plant-distribution in Newfoundland indicated a new interpretation of the continental shelf of eastern America. That interpretation is today accepted without question by our geologists and physiographers. More recently, finding the distribution of plants quite incompatible with the orthodox and unchallenged interpretation of the geologists that the Wisconsin glaciation had completely denuded the median latitudes of eastern North America, I put out a protest. When the first brief abstract upon this new interpretation was published, a geologist at the University which has always been the New England rival of Harvard had the goodness to write me that I did not know what I was talking about. Later, however, when he had the evidence, he was a true sportsman and wrote: "Too much is enough. I am very groggy, utterly nonplussed and quite humiliated." One more personal instance: two years ago, finding that some headlands were a haven for many extraordinarily isolated plants, I propounded to the greatest students of geology in the Great Lake region the question, whether they were possibly nunatacks. Their replies were unanimous: that these areas were covered by the Pleistocene Ice. The botanical evidence, however, was overwhelming, and one of the happiest moments I have experienced at this happy meeting was on Tuesday evening, when, returning without a dry thread upon me from Enfield, I received from the authority upon the Pleistocene, Professor A. P. Coleman of Toronto, the following message: "Some suggestions have been made that parts of the north shore of Lake Superior and other high points near the Upper Lakes show little glaciation. On the Slate Islands [only station between the Rocky Mts. and Gaspé for *Dryas Drummondii*] years ago I was surprised to find no evidence of glaciation." In North America, at least, Pleistocene history must be interpreted anew; in Europe it is being reinterpreted and we may congratulate ourselves that it is the field-botanist who is able to lead the geologist into the clearer paths. The two sciences must draw much closer together; until they do both the historical geologist and the plant geographer will continue to work in unnecessary darkness.

ON THE ORIGIN OF THE FLORA OF GREENLAND[1]

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I. INTRODUCTION

The latest known part of the Greenland flora is that of the northern region, which is quite natural, as this is the least accessible part of the immense country. Thanks to the expeditions which of late have been sent there, rather considerable collections have been brought home from the districts north of lat. 76° N., and further many other parts of the country have, during the later years, been made subject to closer botanical investigations.

Consequently I think that one is entitled to say that the floristic part of the research of the vegetation of Greenland has reached its natural conclusion.

This, however, applies only to the so-called higher plants, namely: phanerogams and pteridophytes, of which considerable new finds are hardly to be expected in the future. Conditions are otherwise as regards the cryptogams (exclusive of the pteridophytes) of whose occurrence only insufficient knowledge is at hand, and this in spite of comparatively many and comprehensive work on the subject. The approximate number of species for each of these groups is 600 bryophytes, 300 lichens, 185 marine algae, 375 freshwater algae, 600 diatoms (marine and freshwater) and 45 dinoflagellates (marine and freshwater); but especially for the microscopical forms, and they constitute the majority, such figures are quite unreliable, and at any rate mere minimum figures.

Any attempt at making phytogeographical reviews based upon the whole of the flora will, therefore, be in vain, and we must rest content with phanerogams and pteridophytes, which as the most conspicuous are also gathered by non-professional collectors.

Further, the distribution of the plants within each of the parts of this extensive country is now presumably rather thoroughly investigated, and in the same manner as no considerable increase of the number of species can be expected for the whole of Greenland, there is no reason to expect great changes in our knowledge of the distribution of the species within the individual parts.

In accordance with the delimitation of species applied by me, the *number of species of phanerogams and pteridophytes for the whole of Greenland amounts to 390*. This is no great number, when considering the size of the country, but it should be borne in mind that the whole of the interior of Greenland is covered by ice, and that the climate is unfavorable to vegetation, both on account of the northerly position of the country and on account of the huge reservoir of cold,

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 19, 1926.

constituted by the inland ice, and finally on account of the encircling cold sea-currents. These three circumstances also contribute towards the comparatively small difference in the vegetation of the north coast of Greenland and that of its southern point, a distance of more than twenty-three and a half degrees of
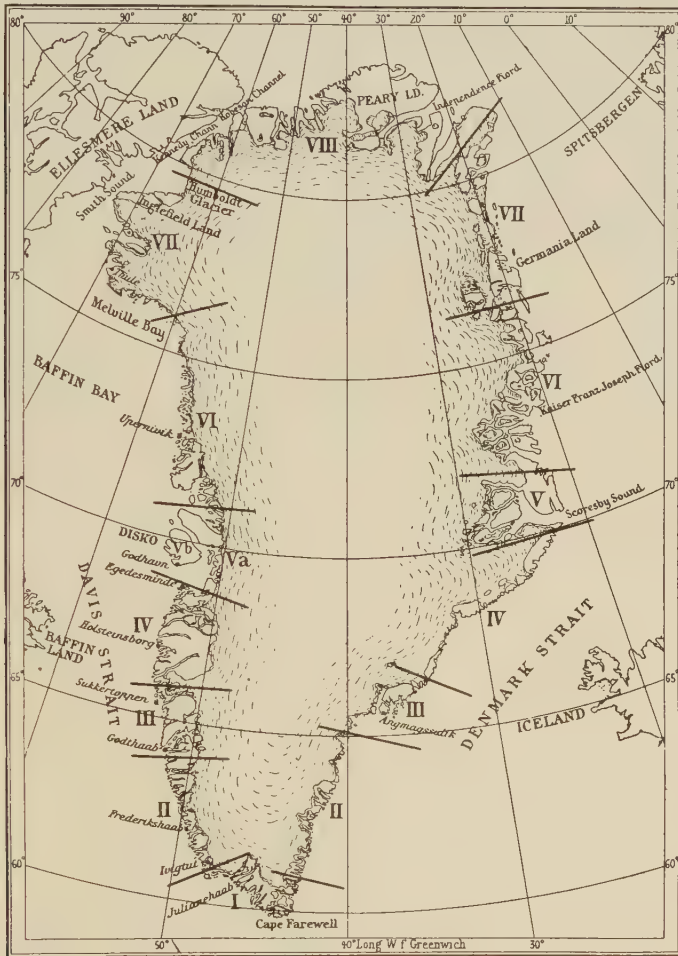
Fig. 1. Map of Greenland showing the phytogeographical districts.

latitude. No less than 32 (8.2 per cent) of the 390 species extend from the northernmost point to the point farthest south, which circumstance in itself is rather unusual, and then these 32 species make about half (42 per cent) of the whole of the sparse flora (77 species) of the north coast.

Nevertheless, there is naturally a much richer flora in the most southerly part of Greenland with its tall birch copses than on the bleak north coast, facing the Polar Sea, with its everlasting cover of ice, the most northerly vegetation known.

With a view to the study of the flora and its distribution it is therefore natural to attempt to divide the country, or rather the coasts, into smaller areas or districts, and this has also been done by the former investigators, as for instance by E. Warming ('88, '91), A. G. Nathorst ('90), and M. P. Porsild ('22).

II. The Age of the Flora in Relation to the Glacial Period

As to the *age of the Greenland flora* this question cannot be answered with any certainty. In the Cretaceous and older Tertiary periods Greenland had a warmly temperate flora, the remains of which are known in part from deposits in central West Greenland (the Vaigat district), this flora being now naturally extinct in Greenland. In Arctic and Subarctic to coldly temperate regions there is, at the present time, a flora whose species for the greater part have a circumpolar distribution. It is a natural supposition that this flora in pre-glacial times lived in the polar regions and was gradually driven south, accordingly as the ice gained the upper hand. The question which interests us in this context is whether the most hardy of the species of this flora, namely, those which at the present time live in the most northerly plant-bearing regions may have survived the maximum of the glacial period in Greenland. I do not mean that they have continued to exist in the same place since before the glacial period, but for instance that by the action of the ice they were driven down to southern Greenland, and from there, at a later period, again migrated towards the north.

This question must, I think, be answered in the affirmative, and this I base chiefly on the find of "higher" plants from the present *"Nunatak"*[2] areas. There is every probability that even during the maximum extension of the inland ice there were "Nunataks," rocky walls, ledges, etc., free of ice, and where their situation was favorable, they undoubtedly were able to harbor a very hardy vegetation. Particularly convincing, it seems to me, in this respect is the occurrence of 8 species in a small Nunatak area near the north coast, in about lat. 81° N. which locality was passed by the Second Thule Expedition in 1916 and called by them "the Midgaardsorm" (that is, the Midgard Snake). The conditions prevailing within this small area are properly speaking those of the glacial period, but in spite of this a few hardy species have been able to live there. They belong to the species which I call *high-arctic* species and *arctic*[3] species. From three other nunataks plants were collected in 1878 by A. Kornerup and J. A. D. Jensen, the latter nunataks being situated at some distance from the margin of the inland ice, in southern West Greenland (near lat. 63° N.) or under much milder conditions, but at a height of between 1000 and 2000 meters. On each Nunatak there were 26–27 species, naturally in part the same; however, the total number of species was 54, of which 40 are arctic, 3 high-arctic, and 11 subarctic and boreal.

These evidences and the circumstance that so very many species occur high

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[2] Nunatak is a greenlandic word which means a cliff or mountain rounded by and emerging from the inland ice and not ice-covered itself.

[3] Definitions of these terms are given later.

up in the mountains,[4] seems to me to make it probable that the hardiest part of the Greenland flora may have been living through the period of the maximum glaciation in the country itself. It is impossible to decide exactly the number of species, any more than what species we are dealing with, but they must first and foremost be looked for among the high-arctic and the widely distributed arctic species, and I suggest that the number of such glacial species in Greenland amounts to about 60. Thus the problem can only be dealt with in its general aspects, not numerically, and it only comes to play a small part in the understanding of the origin of the Greenland flora, the more so as it is more difficult to explain the immigration into Greenland of the less hardy species, which besides are the most numerous. In the subsequent attempt at unravelling the problem of the origin of the Greenland flora I have consequently been obliged to ignore partly the rôle played by these glacial (or pre-glacial) elements.

TABLE 1. PHYTO-GEOGRAPHICAL DISTRICTS OF GREENLAND

	West		East	
	83°—80°	VIII	83°—81°.	
VII.	80°—76°		81°—76° VII.	
VI.	76°—71°		76°—72° VI.	
V a.	71°—69°		72°—69°30.	V.
V b.	Disko		Scoresby S.	
VI.	69°—66°		69° 30—67° IV.	
III.	66°—64°		67°—65°	III.
			Angmagsalik	
II.	64°—61°		65°—61° II.	
	61°—60°	I	61°—60°	

III. The Division of Greenland into Phyto-geographical Districts and the Phyto-geographical Categories of the Plants

In the subjoined table 2 the 390 species are placed in various categories and the country is divided into 15 phytogeographical districts. The number of districts into which the country is divided is naturally a matter of opinion, but I do not think that our knowledge permits of a division into smaller areas than the ones I have given.[5]

In the definition of the districts (see table 1) I have tried to consider the natural geographical and climatic conditions. The most northerly part (district VIII) I have kept separately and so also the most southerly part, which almost coincides with the old Norse "Eystribyggd" (I). This makes 7 districts on the west coast, the Disko Island being set aside as a special area (district Vb) on account of the great number of more southerly forms, which occur in the

[4] See the records of altitude by L. Kolderup Rosenvinge (Medd o. Grönl. 7(3): 1892).

[5] For some of the areas (districts E II and E IV in the southern part of the east coast I have included a number of species which are not recorded from there, but these species occur both to the north and south of the districts mentioned, and *which* consequently, in all probability, are to be found in these districts, which for that matter have not been very thoroughly investigated, and which form very poor habitats for plants, *inter alia* an account of the limited ice-free area.

southern part of the island, and 6 districts on the east coast of which the Ang-magssalik district (E III) and the Scoresby Sound district (E V) each constitute naturally confined areas. The boundaries of the districts, which must naturally only be taken as approximate, are also indicated by degrees of latitude.

TABLE 2.

Distr.	N.		West Greenland						S.			East Greenland N.					Whole Greenl.
	VIII	VII	VI	Va	Vb	IV	III	II	I	II	III	V	V	VI	VII	VIII	
Group A	10	18	17	25	26	30	28	24	24	9	8	6	11	10	8	10	53
B	1	1	1	1	2	1	2	2	2	2	2	1	1	1	1	1	2
C	14	14	15	18	15	10	4	2	2	..	2	4	14	18	13	14	26
D	18	20	30	34	38	36	29	23	22	10	17	18	33	27	18	18	56
E	..	1	1	4	4	9	7	15	24	8	10	3	6	2	2	..	32
F	2	1	1	1	1	..	..	..	..	..	..	..	3	2	1	2	4
G	30	57	90	121	140	155	159	161	184	137	140	97	101	71	53	30	209
H	2	2	..	2	3	4	4	5	5	2	2	..	..	..	1	2	8
Sum	77	114	155	206	229	245	233	232	263	168	181	129	169	131	97	77	390
A_1	44	52	41	43	37	28	9	2	2	..	9	16	39	45	41	44	58
A_2	30	51	94	113	116	114	106	90	85	80	89	85	104	70	49	30	130
S	3	11	20	50	76	103	118	140	176	88	83	28	26	16	7	3	202
W. Grl. only	..	9	8	24	32	48	45	52	87	..	..	..	..	..	..	..	134
E. Grl. only	..	..	..	..	..	..	..	..	..	..	3	1	6	5	2	..	9
Reaching Distr. I.	32	52	93	122	155	172	192	209	263	166	161	102	103	70	49	32	..

Within each district I have counted the number of species and then distributed them: (1) according to their geographical occurrence outside Greenland (A–H), and (2) according to the phytogeographical elements, to which they are referred by this distribution (A_1, A_2, S), further I have indicated, (3) how many of these occur only in western Greenland and how many only in East Greenland, and (4) how many of the species extend as far as the most southerly district (L.).

The division of the species according to their geographical distribution outside Greenland is based upon the floras of the surrounding countries. A species is always referred to the category which approximates it most nearly to Greenland. A species occurring in arctic North America and arctic Asia is therefore classified as American, and a species occurring in Europe, possibly in Iceland, and also in western North America is classified as European.

The categories employed are:

A. Species which occur in northern America, but not in Europe.

B. Species which occur in North America and in Iceland, but not elsewhere in Europe.

C. Species which occur in North America and in Europe, though not in Iceland and Scandinavia.

D. Species which occur in North America and in Europe, but not in Iceland.

E. Species which occur in Europe, but not in eastern North America.

F. Species which occur in Arctic Europe, but not in Scandinavia and Iceland, nor in North America.

· G. Species which occur in North America, in Europe and Iceland (circumpolar species).

H. Species which are not known outside Greenland (endemic species).[6]

Further, according to their general geographical distribution, the species are divided into 3 phytogeographical types (elements). In this the author will naturally have to follow his personal opinion, as there are no sharply distinguished categories and undefined cases are apt to occur. I have preferred to divide them into:

A_1 *High-arctic species*, namely: species which almost exclusively occur in arctic regions, and which are able to live under very severe conditions.

A_2 *Arctic species*, namely: species which are principally distributed over arctic regions, but also occur far outside the latter.

S. *Sub-arctic and boreal species*, viz.: species which are principally distributed outside (south of) the arctic regions; some of these are very well able to live in arctic regions (which probably has some bearing upon the fact, that they properly speaking consist of several microspecies; or perhaps often eco-species in Turesson's sense, others only occur in the most favorable parts of Greenland. From our point of view this category, which properly speaking consists of several other categories, may be looked upon as a single one, and may also be termed "southern element" (which term is for instance used by Porsild ['22]).

The object of indicating how many of the species of each district extend as far as district I is to show partly the extensive distribution of some species, partly the gradual increase in the quantity of species, the latter circumstance, however, being rather a matter of course.

IV. The Number of Species on the West Coast as Compared with that of the East Coast

Special interest attaches to the fact that a larger number of species occurs only in West Greenland, while only a few are restricted to East Greenland.

The great proponderancy in West Greenland as regards particular species, is first and foremost due to the great number of species which occurs in the

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[6] The few species (8) belonging to the latter category occur within the so-called critical genera (*Taraxacum, Hieracium*, etc.). One *Hieracium* has later been found in New Foundland by M. L. Fernald.

southernmost parts (District I), this also including the east coast from lat. 60°
to 61° N., and of which a fairly large part (46 species), as will be shown later on,
is due to the old Norse settlements. But apart from this there is in the southern
part of the west coast far more ice-free country and so also better conditions
for plant life while the distance to the neighboring countries is shorter and the
possibilities of immigration consequently greater. Altogether, 134 species have
been found on the west coast which are not recorded from the east coast, or
about a third of the total flora. On the east coast there are, on the other hand,
only 9 species, which are not to be found on the west coast.

V. Characterization of the Individual Districts

When examining the figures for the individual districts, the following may
be inferred from the table 2.

The number of species naturally increases in the direction from north to
south; some districts are particularly rich in species, viz.: as far as the west
coast is concerned, besides the above-mentioned southern district I, Disko
(district W Vb) and the district directly south of it (W IV) which is distinguished
by its large ice free area and deep fiords. As far as the east coast is concerned, it
has already been mentioned that districts E II and E IV are very poor in species,
partly because there is so little ice-free land, and partly because they are not
particularly well investigated. On the other hand, the large system of fiords,
Scoresby Sound (E V), is comparatively rich, which is especially due to the fact,
that in its inner part, far removed from the cold and fogs of the Arctic Sea, a
number of species occur, which are otherwise not recorded from the east coast,
and which generally do not extend so far north.

The three northern districts, viz.: the north district itself (VIII) and the
adjoining districts on the west and east coast (W VII and E VII) are the poorest
parts; they constitute a very naturally confined whole which I call North
Greenland (north of about lat. 76° N.).

This area comprises 125 species and of these 8 high-arctic species are charac-
teristic of this part and not found elsewhere in Greenland.

Table 2 further shows the interchanges in the numbers of the three phyto-
geographical elements within the individual districts. If for distinctness this
is translated into percentages (see table 3) we get a number of figures clearly

TABLE 3.   PERCENTAGE OF THE 3 PHYTO-GEOGRAPHICAL ELEMENTS IN THE VARIOUS DISTRICTS

	West							South				East			
	VIII	VII	VI	Va	Vb	IV	III	II	I	II	III	IV	V	VI	VII	VIII
A_1....	57	46	26	21	16	11	4	1	1	0	5	12	23	34	42	57
A_2....	39	45	61	55	51	47	45	39	32	48	49	66	62	54	51	39
S.....	4	9	13	24	33	42	51	60	67	52	46	22	15	12	7	4

A_1=High arctic. A_2=Arctic *sens. lat.*   S=Sub-arctic and boreal.

illustrating the fact, that the number of high-arctic species, which constitute 57
per cent of the total number of species in the district VIII gradually drop to
1 per cent in district I (district E II has 0 per cent, but this has undoubtedly

some bearing upon the above-mentioned poverty of the district) and that the number of the sub-arctic and boreal species (the southern element) increases from 4 per cent in district VIII to 67 per cent in district I. This is what might be expected. It is, however, interesting to note the circumstances relating to the common, widely distributed arctic species; they are most numerous in districts W VI and Va and in E IV and V, where we find the conditions which are particularly favorable for their occurrence; the number of species drops from these two maxima both towards the north, where its minimum is in district VIII, and towards the south, with minimum in district I. This distribution of their percentages in the flora points in the direction that the rough estimation of them as arctic species in a wider sense in contrast to the high-arctic species proper as well as to the subarctic species has been essentially correct.

VI. The Immigration of the Species

From table 2 we may deduce several considerations as to the *distribution* of the Greenland species *outside Greenland*. The bulk (G) have a circumpolar distribution which in itself does not show anything as to whence they have immigrated into Greenland. The few endemic species (H) have already been mentioned.[7] Now the species remain whose distribution outside Greenland is not circumpolar; for these the distribution should give us a hint as to whence they come.

The species of the categories A (53) and B (2) may be reckoned as coming from America and E (32) and F (4) as coming from Europe. We are confronted with greater difficulties in the case of group C (26 species) which partly comprises a few subarctic and boreal types (4), in all probability immigrated from America; partly some high-arctic (17) and some arctic (5), which may just as well have come to Greenland from Spitzbergen as from arctic America; in the case of some of the latter their occurrence within Greenland may show whence they have probably come: namely, 4 from the west and 1 from the east; as to the remainder (17) nothing can be said with certainty; they may have survived the glacial maximum in Greenland. Similar conditions apply to group D (56 species). Here 20 must be reckoned as having in all probability come from America and 6 from Europe, some (4) of which, however, belong to the subsequently mentioned plants from the old Norse colonization. There then remain 30 species of uncertain origin (partly preglacial).

According to these considerations 87 species can with probability be said to have immigrated from North America. Of the remaining 209 circumpolar species 26 according to their distribution in Greenland can certainly be thrown into the balance in favor of America which makes up 113 American species. To this must be added, however, as a very important circumstance, that when a species according to its distribution in Greenland as well as outside Greenland, may just as well have come from America as from Europe, the greater proximity of America makes its immigration from America probable. Consequently, there

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[7] It is probable that the 4 *Hieracium* species are derived from European parents, while the other 4 species have American relations.

is no doubt that the figure 113 (29 per cent) is a minimum figure, which certainly ought to be much greater. The European contingent on the other hand consists of 74 species (19 per cent) of which 50 are old Norse plants (15 of which are included in the figure 32 of Group E and 4 in Group D).

The remainder of the flora, that is, 203 species (52 per cent) do not give any direct indication as to their origin, but as said above it is more probable that they have come from North America, apart from the unknown number of surviving preglacial species (guessed to be about 60 species).

The distribution of the species within the individual districts offer several points of interest, as will appear from the tables. The pronouncedly American species are comparatively well represented in the most northerly part of West Greenland, as several of them are naturally high-arctic. On the other hand, a number of the American species occurring in the more southerly part of West Greenland are subarctic and boreal types; several of these really belong to the forest regions of northern America.

Of species which have immigrated to East Greenland may be mentioned some European high-arctic types in the most northerly part and a few sub-arctic and boreal ones at Angmagssalik.

On the other hand, it is worth mentioning that there are, naturally, species in Greenland which are widely distributed over the whole of the country—we have already referred to the 32 which are to be found all the way from north to south—and other species whose distribution is more limited. The rarest species are those which have been found only in a single place; further, a not inconsiderable amount only occur in one district although in several places there. Particularly rich in such rare species is the southern district (I) which has 36 separate species. From there it is a great distance to district W II, which has 6 species, W IV which has 4, W III which has 3, W VII, E III and E V each with 2, and W VIII and E V with 1 species each. Species of such limited distribution must rather be supposed to have newly immigrated, whereas those which are widely spread must be supposed to have lived in Greenland for a longer time. Among the pronouncedly American species there are some which furnish excellent illustrations of all these circumstances.

As to the ways by which the species may be supposed to have immigrated into Greenland a few words may be said. The distance between North America and Greenland is shortest towards the north in Smith Sound and Kennedy Channel, and it is a natural supposition that this approach has been greatly used and is still used by the plants: thus two species of *Pedicularis* are in Greenland only to be found in Inglefield Land, having probably in recent years immigrated from Ellesmere Land, from which they are recorded, but otherwise they occur in the whole of arctic North America. As a matter of course particularly the high-arctic and arctic species have followed this route of immigration, and some of them have merely gone to the south in West Greenland, whereas others have gone northwards and then down the east coast.

In 1905 Ad. S. Jensen and P. Harder proved the existence of some layers of shells in the Vaigat district about 70° Lat. N., where remains of bivalves oc-

curred, which at the present time are not to be found in Greenland, their northern boundary at the present day being at the Gulf of St. Lawrence. As these layers of shells are considered postglacial, these bivalves are indubitable evidence of a warmer post-glacial period, during which a number of species of American plants, which at the present time are not supposed to be able to immigrate by a route as northerly as across Smith Sound, may have used this approach. At a later period they have then been driven further south.

However, even in more southerly localities West Greenland has received a fair contingent of American species, especially the sub-arctic and boreal types, which must have come across the Davis Strait, probably chiefly from Baffin Land and Labrador.

If we then turn to East Greenland, there are farthest north some species which must have come across from Spitsbergen and other arctic islands of the neighborhood, and farther south, in the Angmagssalik district, we meet a small number of species, which must be supposed to have immigrated from Iceland.

The manner in which all the species have been able to immigrate is a problem which in many cases is by no means easy to solve. The natural methods of immigration are by the agencies of water, wind and animals. As far as Greenland is concerned the water, in its usual fluid state, has no great importance as a medium of immigration, seeing that only very few species of shore plants occur. On the other hand, special emphasis must be laid upon its great importance when in a frozen state. Where the sea ice lies solid during the winter, it forms an excellent highway, along which seeds and pieces of plants may be carried by the wind, which at that very season often blows with particular strength. A distance like the one across Smith Sound is nothing when there is a cover of ice. If, on the other hand, the ice is carried along by currents, as frequently happens off the coast of East Greenland, it is certainly also possible that plant material may be carried along from other countries, and this explains the occurrence of easterly arctic species in the northern East Greenland; several of the characteristic species are even limited to the outermost coast belt, which seems in favor of this supposed manner of immigration.

The part played by the wind in the dispersal of the seeds within these regions is undoubtedly very great, particularly in winter, when the surface is covered by snow or, as just mentioned, by ice. Most Greenland species have rather small seeds.

Finally, as regards carriage by animals or, rather, by birds, several of the species have fleshy fruits, which spread through the agency of the birds, which also in other ways, when wandering between Greenland and the coasts of North America may further the immigration. Consequently, I do not think, that as far as Greenland is concerned it is necessary to have recourse to land bridges in order to explain immigration.

VII. THE BOTANICAL IMPORTANCE OF THE NORSE COLONIZATION

In conclusion, mention should be made of the part which the *Norse colonization* of Greenland (extending over a period of 400–500 years from 985 or 986

A.D.) must be supposed to have played in the composition of the flora of southern Greenland. As to this no direct information is at hand. The old sagas are curiously reticent as regards what was carried by the vessels, by way of food for men and animals, but we know that the seafarers had living cattle and sheep on board. The provisions in all probability consisted of grain (flour), salt meat, and then the living cattle which might supply milk and butter. But these animals, in their turn, must be fed with hay, from which it may be concluded that the vessels would carry very considerable quantities of this commodity. When they arrived at their destination, the vessel must undoubtedly have been cleaned and brought ashore for the winter and the offal from the hay-fodder might then easily be thrown away, and so there was a possibility that some of the seeds which had been brought along might come to rest in places where they were able to germinate. Further, this hay-offal must be imagined to have been very diverse, as the sowing of pastures with one or only a few kinds of seeds was unknown in those days. For that matter it is so even now in Iceland and partly in Norway, which two countries must be considered the purveyors of the hay and seeds, since nearly alone they have kept up the communication with the Norse settlements.

The cattle and sheep which the seafarers carried with them was, however, not only to serve as food during the journey; there were also live cattle to be taken ashore in Greenland, a natural consequence of the fact, mentioned in detail by the Icelandic professor Finnur Jonsson (1893), that the raising of cattle and sheep played a great part in the economic life of the old Norsemen, and the information given in the "King's Mirror" to the effect that "much butter and cheese is made." Also the ruins found of the old habitations show that the farms, like those of Iceland, were surrounded by fenced-in yards (tun).

Everything considered, there is thus much indirect evidence that there has been ample opportunity of carrying seeds from Europe (particularly Iceland and Norway) to Greenland, and in the present flora there are several species (for instance *Vicia cracca*) which keep strictly to the immediate surroundings of the old farms, particularly the old bishop's seat Gardar at Igaliko. That these species owe their occurrence in Greenland to the old Norsemen, of that there can be no doubt; but it is more difficult to say anything for certain as regards the species which have thrived better and which in the course of centuries have had the opportunity of spreading and coalescing with the original vegetation. In the case of the latter all that can be arrived at are more or less well-founded suppositions.

Plants which may possibly come under the category "old Norse plants" should have a distribution corresponding with the areas of the old settlements, which are now well known, thanks particularly to the comprehensive researches of the Danish explorer, Daniel Bruun. Further, they should be species living in Iceland or Norway, and finally their habitats should be such that it is possible to think of them as having been imported with hay from meadows and grass-lands. There are in all about 50 species of phanerogams,[8] which may be said

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[8] I do not include the pteridophytes which have the same distribution, as their small and light spores make them more fit to be spread by the agency of the wind across great distances.

more or less to comply with these conditions, which from the point of view of distribution means that they principally occur only within an area from the most northerly part of Godthaabsfiord in the north, southwards to Lindenow fiord in the very most southerly part of the east coast, that is, corresponding with the phytogeographical districts W III–I. Most of these are meadows or grass-land plants and no less than twenty are grasses or grass-like plants. The greater number of these species occur only in district I, which corresponds with the old "Eystribyggd," the largest old settlement. Several of those which extend further north are lacking in district II and only recur in district III, Godthaabs-fiord, the old "Vestribyggd." Consequently it may be estimated, with a certain degree of probability, that almost an eighth of the Greenland flora (nearly 13 per cent) has been brought to Greenland by the old Norse settlers.

As mentioned above (page 1516) these species must be added to the number of species which have immigrated from Europe, in which manner a *total of about 74 European species (19 per cent) is obtained*. Thus roughly calculated there are about 316 species (that is, four-fifths of the whole of the flora) *which must be supposed to be of American origin, or, for the smaller part to have survived the maximum of the glacial period in Greenland.*

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[9] A more detailed paper dealing with the same subject has just been published, compare Osten-feld C. H. The Flora of Greenland and its origin.—D. Kgl. Danske Vidensk. Selsk., Biolog. Medd. 6(3): 1926. In this paper also the names and distribution of all the phanerogams and pteridophytes of Greenland are given.

ENDEMISM AND ITS SIGNIFICANCE IN THE CALIFORNIA FLORA[1]

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The flora of California is made up of four floral elements: the Boreal which occupies the higher altitudes of the mountains, the Mexican or Sonoran which predominates in the deserts of the southeastern part of the state, the Great Basin which flanks the eastern base of the Sierra Nevada, and finally the Californian which occupies the foothills and valleys throughout the Pacific slope area of the state, that is from the western slope of the Sierra Nevada divide to the coast.

It is often stated that this California element is of recent origin, probably mainly post glacial, formed by the commingling and modification of the Mexican and Boreal elements. But an analysis of the flora and a study of the geological records point clearly to the conclusion that the California element is not essentially of recent formation. There was in all probability less change climatologically and floristically in coastal California during Glacial and Post Glacial time than in the interior and eastern part of the continent.

The differentiation of the California element we hope to show is to be found then not in recent or post glacial time, but rather in Tertiary and even Mesozoic time.

In analyzing a floral element it is important to study particularly old or relic species and genera, and also the plants whose close affinities are with those in regions widely separated geographically. The presence of either sort in any goodly number suggests an origin in a more or less remote past.

Asa Gray ('59, '72), in his classical papers—the "Flora of Japan" and the "History of the Sequoia"—has shown that the surprisingly close relationship between the floras of eastern Asia and eastern North America is traceable to Miocene time. The beautiful deciduous forests of the eastern states are in many cases the direct descendants of these ancient Miocene forebears. *Liquidambar* and *Liriodendron*, as well as some of the oaks, maples, and other plants have very closely related species in far away eastern Asia. It is this phase of the California flora I wish to discuss first.

In California, sequoias are found in the rocks of every geological age since the Lower Cretaceous, except the Upper Oligocene, in which only marine deposits are represented.

The presence of sequoias in the California flora always has been of especial interest to the student of plant distribution. But that the genus has persisted there since the middle of the Mesozoic is even of greater significance.

[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 19, 1926.

A study of the marine fossils of the California rocks points to the fact that the Pacific Ocean along the California coast never has been much colder, even in the Glacial Period, than at present. And the presence of sequoia fossils in the freshwater deposits points to the same conclusion and indicates that the Pacific Ocean, throughout these ages has exerted the same ameliorating influences on the climate that it does today, with the result that the climate of the coastal region is and always has been oceanic with no marked seasonal changes in temperature.

The climatological history of California therefore is quite a different story from that of the interior and eastern part of the North American continent. There, following the elevation of the interior and the consequent retreat of the great sea which formerly stretched from the Gulf of Mexico to Hudson Bay, we had the beginning of a continental climate in the late Cretaceous time, with the accompanying marked changes in seasons. The culmination was the great broad-leaved forests of Miocene time which spread over North America from the Cordilleras of the Pacific to the eastern rim of the continent and even extending to the Old World.

The close relationship brought about by the former intermingling of the floras of the two continents in the northern hemisphere, as pointed out by Dr. Gray and others, is evident to anyone. Many of our most familiar genera are common to both hemispheres. It is further well known that the arctic and subarctic floras are more closely linked than are those of the temperate; and those of the cool temperate more so than those of the warm temperate and subtropical. From this as well as from the geological records it is evident that the bridge or bridges connecting the two continents possessed a mild climate which eventually became cool-temperate and finally arctic.

If this hypothesis be true California with its long period of mild equable climate should possess a flora less closely related to that of the Old World than is that of the eastern part of North America. California should also have a greater number of American or endemic genera. And such genera as are peculiar to it and the Old World we might expect to be of an older type.

This brings us back to the thought that must have occurred when it was first realized that sequoias have persisted in California through so many ages, and that is, are there not other relics of the mesozoic or early tertiary floras associated with them?

Definite evidence is rather meagre. First of all what are old types? We are still very much in the dark concerning the relative age of the living plant genera.

But taking up first the ferns we find *Equisetum telmateae* common to the Old World and the Pacific Coast, also *Struthiopteris spicant*. When these plants crossed over the intercontinental bridges we do not know, for we have no definite records. The genus *Woodwardia* however offers more definite data. This is a genus of 4 or 5 species, with all but one belonging to the Old World. The single North American species is on the Pacific Coast and mainly confined to California. Fossils of *Woodwardia* occur in western America in the Upper Cretaceous, Eocene, Miocene, and Pleiocene times, and are found as far east as

Colorado. *Woodwardia* then is clearly an old type with its connections with the old world going back at least to late Mesozoic.

Among the gymnosperms, besides the classical illustration of the *Sequoia* the most interesting example of an ancient relic is the genus *Tumion* or *Torreya*. Like the sequoias, this genus was once wide spread over the northern hemisphere, but is now reduced to four isolated relic species. One of these is in California, where it is commonly associated with the sequoias, another in Florida, and the others in China and Japan. *Cupressus* or the true cypresses belong to the warm temperate region and are common to southwestern United States (especially California, which has six species), to Mexico, the Mediterranean Region and southern Asia. *Libocedrus* is essentially a genus of the southern hemisphere, occurring north of the equator only in southern Asia and in California. The Californian species is a very distinct type and is set off as a separate subgenus or by some as a distinct genus. The fossil records are few and I have not been able to verify their authenticity, but certainly the segregation of the Californian species from the other members of the group must date at least well back in the tertiary and probably earlier times. *Pseudotsuga* has six species, two in China, two in Japan, one widespread over western North America, and the fourth a geographically restricted species in southern California.

Turning to the Angiosperms we find a comparatively large number of genera common to California and the Old World, but not occurring in eastern North America. *Lithocarpus* or *Pasania* is a large Asiatic genus of over 100 species, which is confined to the warm temperate and tropical regions. A single species is in the New World and is restricted to the California Floral Province, being at its best in the redwood belt. *Castanopsis* presents almost the same story, with 30 species, two of which are on the Pacific Coast, the rest in Asia. *Mahonia* or *Odostemon* has a similar distribution, being Asiatic and West American.

And so we might go on naming a long list of genera common to western North America and the Old World, but not found in eastern North America, but enough have been listed to bring out the point under discussion.

As to when these plants migrated, the recent work of Chaney ('24) throws considerable light. In studying the plant remains of the Bridge Creek formation, which is Upper Eocene or Lower Oligocene, Dr. Chaney found a sequoia forest flora very similar in composition to that of the redwood forests of today. The predominating fossil was *Sequoia langsdorfii*, the progenitor of the redwood, *Sequoia sempervirens*. Associated with these sequoias were most of the genera I have just been discussing, that is, *Lithocarpus*, *Mahonia*, *Castanopsis*, and *Tumion*. Among them also was the endemic genus *Umbellularia*, a member of the *Lauraceae*.

Hannibal ('11) found in the Santa Clara beds, which are Pleiocene, a flora essentially the same as that of the present time. Such characteristic present day species as *Sequoia sempervirens*, *Arbutus menziesii*, and *Quercus chrysolepis* were frequent in these beds.

The work of Chaney and Hannibal permits us to say with considerable degree of confidence that many of the more characteristic and dominating plants

found in the redwood region have been associated with the sequoias at least since the early Tertiary. And that the flora of the redwood so far as its chief components are concerned is not of recent origin, but dates back to early Tertiary and probably to Mesozoic time.

This brings us to the main topic under discussion, that of endemism.

If California as we have tried to show has possessed a climate unlike that of other parts of North America through so many ages and has been well walled in by both climatic and physical barriers, is it not logical to expect the flora to be rich in endemics? For the greater and longer the isolation the more distinct a flora becomes.

This thought may seem to run contrawise to the "age and area" theory, if that theory is accepted without taking into account such factors as isolation. In fact, endemism and restricted distribution has been the argument used to support the theory that the California flora is recent, but I am convinced that endemism in California is due, at least in large part to a long period of isolation, both physical and climatological, and that the endemic genera are not essentially recent.

At any rate endemism is highly developed and endemic genera occur among most of the plant families from the lower monocots to the composites. Even in the gymnosperms there are endemic pines that must extend well back in the Tertiary. The very distinct groups known as heavy-cone pines—*Pinus sabiniana*, *P. coulteri*, and *P. torreyana*, although restricted in their distribution must be of ancient vintage, for they are strikingly distinct from the other pines. The close-cone pines are also a distinct group of California species, one of which at least, *Pinus radiata*, dates back to the Miocene, and perhaps further.

In the *Liliales* there are a larger number of endemic genera, some of which such as *Odontstemon*, *Chlorogalum*, and *Scoliopus* are very distinct types. In the Polygonaceae the American or essentially west American tribe, Eriogoneae, is well developed in California. All of the eight genera are present and some are restricted to the state. The poppy family is especially well represented. *Platystemon*, *Meconella*, *Romneya*, *Dendromecon*, and *Eschscholtzia* are endemic to western North America, and are mostly confined to California. It is interesting in this connection to note that two Old World genera, *Papaver* and *Meconopsis* have each an endemic species in California. The Sarraceniaceae is represented by an endemic genus *Darlingtonia*. In the Rosaceae the tribes Potentilleae and Cercocarpeae are chiefly West American and perhaps most highly developed in California.

The Tubiflorae especially the Polemoniaceae, Hydrophyllaceae and Boraginaceae are abundant in the California element. In the family Hydrophyllaceae, for instance, there are 17 known genera and approximately 170 species. Of these, 13 genera and about 90 species are in California.

The California flora is also rich in composites. The tribe Mad'eae is almost entirely confined to the state—a few extend to Chili and one to the Hawaiian Islands. The tribe Inuleae offers a very interesting distributional problem. Several genera are endemic, some are common to California and the Mediter-

ranean regions, others to California and Chili. There is some significance to be found in the fact that in each of the regions of the world which has a warm semi-arid climate, such as California, Chili, Australia, South Africa, and the Mediterranean region the Inuleae have developed a group of endemic genera. This world wide distribution and differentiation has taken time, longer I think than that of the post glacial.

In conclusion we would set forth the propositions.

First. That California from its geographical position, from its geological records, and from the floristic composition of its flora, has been ever since its beginning in the Mesozoic time, a more or less distinct climatological and geographical unit, more or less shut off from the rest of the continent.

Second. That the flora contains a number of relic genera, as well as genera common to it and the Old World, but not occurring in eastern North America.

Third. The geological records show that most of these genera have been in western America at least since early Tertiary and in some cases since the Mesozoic.

Fourth. That the flora contains a remarkably large per cent of endemic genera and species for a continental area a fact which is to be attributed to the long period of climatological isolation.

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SOME EARLY 18TH CENTURY AMERICAN COLLECTIONS AND THEIR COLLECTORS[1]

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When the Executive Committee of the Congress honored me by an invitation to read a paper, I tried to think what subject with which I was in a position to deal would be of some interest to an audience composed largely of American botanists. The historical side of botany is, I know, appreciated by American botanists. We have in the Department of Botany of the British Museum a number of early American collections; many of these form portions of the herbarium of Sir Hans Sloane; others formed part of the collections of Sir Joseph Banks, which were bequeathed to the British Museum at his death in 1820.

Many American botanists have personally consulted these collections, but for those who are not familiar with them a few words of introduction may be useful. Sir Hans Sloane, Bart. (1660-1753) was a man of great eminence in the scientific and medical worlds; he was elected a Fellow of the, then young, Royal Society of London, in 1685; and for thirteen years, 1727-40, was President: for sixteen years he was President of the Royal College of Physicians. During his long life, of 93 years, he accumulated large collections of objects of natural history and art, a library, and manuscripts, which at his death became the property of the nation and were the foundation of the British Museum in 1756. His herbarium, with which alone we are now concerned, is contained in 334 volumes mostly in large folios on the leaves of which the plants are pasted. At the age of 27 (1687) Sloane went to Jamaica where for sixteen months he assiduously studied the natural history of the island. The results of his work were published in his "Natural History of Jamaica," in two large quarto volumes (1707, 1725), a work notable as the first really scientific account of the natural history of a portion of the New World. The plants are preserved in seven volumes and formed the foundation of his herbarium, which he increased throughout his life by the incorporation of numerous collections obtained by purchase or gift. The number of his plants was greatly under-estimated at the time of his death, by his trustees as 12,506. Sloane's copy of Ray's "Historia Plantarum" forms an index to the collections; it contains references to the herbarium in Sloane's hand, and corresponding references to the "Historia" are written in the Herbarium.

Among the collections acquired by Sloane were those of James Petiver (c. 1658-1718), who was apothecary of the Charterhouse, F. R. S., and a great collector. He got in touch with merchants, ships' captains, and surgeons, and from

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these correspondents received collections from many parts of the world. His "Hortus Siccus Americanus" occupies three volumes of Sloane's Herbarium. He published an interesting little volume called the "Museum," in which the items of his collection are catalogued.

A second large collection acquired by Sloane was that of Dr. Leonard Plukenet (1642-1706), who had a botanical garden at Old Palace Yard, Westminster, and was Queen's botanist to Mary II. Many of his plants are figured in his "Phytographia," in 1691, and these figures are mounted with the specimens in his herbarium. The importance of the collection is evident from the fact that Plukenet's figures were largely cited, especially by Linnaeus in his "Species Plantarum."

Some of these early collections are well known to American botanists—as, for instance, those of Mark Catesby (1679-1749) the author of the "History of Carolina" (1730-48), and of the Rev. John Banister, missionary in Virginia, whose untimely death from a fall when collecting, about 1692, "increased the list of martyrs to natural history" (Pulteney, "Sketches" 2: 55.). He sent to Ray in 1680 a "Catalogue of Plants observed in Virginia," which was published in Ray's "Historia" 2: 192. These plants are in the Sloane herbarium. Familiar also is the collection of John Clayton who went to Virginia in 1705, and whose specimens are described in the "Flora Virginica," 1739-45. He sent his plants to Gronovius, the friend of Linnaeus, in Holland. The collection was subsequently bought by Lord Bute for £100, and, ultimately, at the sale of Lord Bute's effects, by Banks (for 42 guineas), as was also William Young's (fl. 1753-84) volume of "South Carolina" plants. A contemporary collection from Carolina, that of Thomas Walter (1740-88), the author of "Flora Caroliniana" 1788, is also at the British Museum.

I propose to refer to a few collections which are probably unfamiliar to American botanists, and which will indicate possibilities as to earliest records which should interest those engaged on floras of restricted areas.

Rev. William Clerk (fl. 1710-1734). Herb. Sloane, vol. 60, ff. 116-118. This is a small collection labelled "Musci ex Virginia allati 1729 a Do. Clerk V. D. M.," mostly lichens, also a specimen of *Tillandsia usneoides* and male inflorescences of *Taxodium distichum*.

Herb. Sloane, vol. 240. ff. 63-100. "Plants gathered in Virginia by Mr Clerk." An interesting collection of several hundreds of plants arranged by months from March to September 1729, evidently by Clerk himself, as the month is indicated in a neat handwriting on the sheet. The specimens are small, sometimes consisting of little more than a flower or inflorescence but are determinable. There are no original labels but Sloane has referred some to Ray; for instance, a specimen of *Silene stellata* Aiton bears the indication R. S. 489 (in Sloane's hand), that is, Ray "Supplement," 489, *Lychnis Caryophyllea virginiana,* which had previously been sent by John Banister from Florida and figured by Plukenet ("Phytographia," t. 43, f. 4. 1691).

Folio 76 contains the following representatives of April flowering plants.—*Cypripedium pubescens* Willd., *Azalea viscosa* L., *Sarracenia flava* L., *Panicum Crus-Galli* L., *Aquilegia* sp., *Anemone thalictroides* L., *Stuartia malacodendron* L., *Hypericum mutilum* L., *Cornus paniculata* L' Hérit.

Folio 94, July. *Oxalis stricta* L., *Desmodium paniculatum* L., *Bidens cernua* L., *Asclepias incarnata* L., *Polypremnum procumbens* (Loganiaceae), *Campanula americana* L., *Abutilon Theophrasta* Medic. (*Sida Abutilon* L.,) *Coreopsis verticillata* L., *Pycnanthemum aristatum* Mich., *Decodon verticillatum* Ell. (Lythraceae), *Silene stellata* Ait.

Vol. 296. "Rare plants gathered in Antigua and Montserrat in the year 1734 and brought from thence by the Rev. Mr Clerk." The specimens are unnamed.

Vol. 318. ff. 1-56. "Plants and Submarines gathered at Carolina Bermudas and the Caribees by the Rev. Mr Clerk." There are no original tickets and the localities are not distinguished in any way; among the specimens is the Bermudan *Erigeron Darrellianus* Hemsl.

Joseph Lord (fl. 1701-1711) of Dorchester, Carolina. "Plants from Carolina by Mr Job. Lord" are in Herb. Sloane, vols. 263, 284 (ff.40-91), 285 (ff.1-8), and others. Both in the Herbarium and by Petiver ("Gazophl." 96, where there is a list of Carolina plants from him) his name is given as Job, but his letters in the Sloane Mss. (4063,4) are signed "Joseph." The specimens which are well preserved were gathered in 1704; with each is a descriptive label in Lord's beautiful, neat hand giving information as to habitat, characters, and date of collection, indicating that Lord had some botanical knowledge. In vol. 285. f.4, a leaf specimen of *Sarracenia flava* has this label, "This is a differing species of ye plant w^h Gerard calls hollow Sea Lavender (or at least Johnson upon Gerard) and Limonio congener". Johnson in his edition of Gerard's "Herbal" (1633) p. 412, merely copies the figure and description from Clusius ("Historiae Plantarum" lib. 4. p. 82, 1601), who received the figure with one dried leaf from Claude Gonier, an apothecary of Paris, who himself had received the dried plant from Lisbon. The figure represents a leaf rosette of *Sarracenia purpurea*. Clusius calls it *Limonium peregrinum* and notes that he has no information as to what the flowers or seed are like, or as to its native place or time of flowering. Johnson hopes "that some or other that trawell into forraine parts may find this elegant plant and know it by this small expression, and bring it home with them, that so we may come to a perfecter knowledge thereof."

If Lord had been familiar with Plukenet's "Phytographia" (1691) he would have found figures, t. 152.f. 3, and t.376. f.5, not unlike his plant under the name *Bucanephyllon elatius virginianum* s. *Limonis congeneris altera species elatior*, etc. The specimen of the second in Herb. Sloane (v. 93. f. 74) has been determined by Prof. J. M. McFarlane as *S. flava* x *S. purpurea* (Journal of Botany 1907, p. 4).

On the same sheet is an orchid, *Platanthera ciliaris* Lindl. Lord's long and numerous letters to Petiver are full of interesting and detailed observations on the zoology and botany of his district. "The only book y^t I have y^t describes Herbs" he says "is Culpepper's 'English Physician.' Some hints I meet wth occasionally in reading by wch I gath^r some knowledge elsewhere." His nearest neighbour, Daniel Henchman, also collected "haveing been himself more than 300 miles in the countrey." Henchman died in November, 1709; he intended to have sent his collection to the Royal Society, but there seems to be no record of them.

Three collectors in Maryland whose plants are associated in Herb. Sloane, where they are generally indistinguishable from each other, are William Vernon (fl.1688-95), David Krieg (d. 1712-13) and Rev. Hugh Jones (1675-1758). Dr. David Krieg is described by Petiver ("Museum," 45, 1699) as "a German Physician and Fellow of our Royal Society. This curious Gentleman, after he had made several remarks on the Natural Productions of this Island, [that is, Great Britain] and painted several things he had here observed; was pleased to make a Voyage to Maryland, from whence he returned plentifully stored with what in Nature he had there taken notice of. His happy Genius in Designing, Painting, Etching, etc., were no small Additions to his other Qualifications; he being no less versed in the study of Physick, than Anatomy, Botany, Chemistry, Natural Philosophy, and indeed whatever else is requisite to compleat a Physician."

Krieg went with Vernon to Maryland whence he brought plants to Plukenet who styles him *"medicus ornatissimus"* ("Mantissa," 81); these plants are doubtless in Plukenet's Herbarium but are not indicated. His plants are in several of the volumes of Herb. Sloane. Vol. 74 contains plants from all three collections, Krieg, Vernon, and Jones under one heading; "Plants gathered in Maryland by Mr Jones, a minister, Dr. Krieg and Mr Vernon, and by them given to Mr Ayrie. Extraordinary good specimens, well preserved, and the greater part referred to Mr Ray". The three collections are not separated but the collector's name can be ascer-

tained by consulting the Solander[2] Mss. where the specimens are referred to and some are described as new species. Solander named the collection throughout and indicated the then novelties by adding "Mscr." to their names. Thus a specimen from Krieg on f.45 is the plant figured by Plukenet (Phytogr. t.13.f.4) on which Elliot in his "Botany of South Carolina" (2:114) established his *Gerardia Plukenetii.* Many of Solander's descriptions of these specimens were taken up in Aiton's "Hortus Kewensis." Thus *Fagus ferruginea* Mscr. (f.5) is described in the Solander manuscript (where the specimen is assigned to Jones) and was published in "Hort. Kew." 3:362, though no reference is made to Jones. On f. 8 (and also in Herb. Sloane 159.f.111) are specimens collected by Jones from which Solander in his manuscript described the genus *Comptonia,* published in "Hortus Kewensis" 3:334. 1789. There has been considerable confusion as to the authority for this genus; the matter was cleared up by the late James Britten in the "Journal of Botany" (47:45).

Many of the specimens in Herb. Sloane 158 (Petiver's American Collection) have labels (some dated 1700) in Krieg's hand, for example, the Composite *Anaphalis margaritacea* f.128 "this plant has a strong physicall Smell, and ye Indians put it into a deer's head when they hunt. A decoction of it is good for ye feavor. I never see it grow, it was given me by an Indian who could speak but little English and so could get no further account of it." To this is added a note in Petiver's hand "With this ye Indians rub ye heads and affirm it is [good] for the eyesight. Lawson" Other labels show that Krieg had observed the habits of plants and had some botanical knowledge. Some of Krieg's specimens are in Herb. Banks, for example, *Cypripedium pubescens* collected in 1698; and he also sent plants to Oxford to Bobart. Krieg was in England in 1699 (Ray Correspondence 365); his plants were sent by Sloane to Ray for description with those of Vernon and are acknowledged in the preface to vol. 3 of the "Historia" (p. 3). He was elected F. R. S. in 1798. Solander in his manuscript (4474) named a genus, which he had previously called *Forstera,* in his honour; the specimen which was collected by Catesby in Carolina (Herb. Sloane 212.f.33) is *Helenium nudiflorum.*

Krieg's letters (in English) to Sloane and Petiver (1699-1708) contain interesting matter. He left London, where Sloane had shown him much kindness, in 1699 and went to Riga where he took up practice as a physician, although he "never found that contentment there" which he had with Petiver, with whom he apparently lodged, as he speaks of him as his "good Landlord". In 1700 he visited Stockholm, Copenhagen, and Hamburg on his way to Paris, where he stayed until 1703 when he returned to Riga. In Paris he made the acquaintance of the leading botanists Geoffroy, Plumier, and Vaillant.

Herb. Sloane vol. 37 is described as a "Book containing about 250 plants gathered in Maryland by Dr. Krieg and plants gathered in Maryland by M[r] Vernon, with notes and observations upon them by Mr Ray, Dr. Amman, Dr. Krieg, etc." Many of the specimens from f. 61 to the end are named by Ray and many are referred to in his supplement, for example (f.38), "28 *Eupatorium Virginianum* [*E. perfoliatum* L.,] . . . . *Hujus specimen siccatum nobis communicavit* D. Sloane *à* D. Vernon *è marilandia allatum*" (Suppl. 189). Many are also named by Solander. The two collectors are not discriminated in the volume but Ray seems to have known which plants were collected by each, as he quotes their names.

William Vernon was a Fellow of St. Peters College, Cambridge (he graduated B.A. 1688, M.A. 1692). Dr. Richard Pulteney ("Biobraphical Sketches", 2:57 1790.) refers to the herbarium of several hundred new and undescribed plants collected by Krieg and Vernon in Maryland which "came into the possession of Sir Hans Sloane, by whose liberal communication they were inserted in the "Supplement" to Ray's "History." In Ray's correspondence (p. 362) is a letter dated March 22, 1698-9, from Ray to Sloane referring to the Maryland collection of Vernon and Krieg which Sloane had just sent him. "I was was very much taken with the beauty of the dried plants, indeed I cannot say that ever I saw the like spectacle: such large

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[2] Daniel Charles Solander (1736-82), the favourite pupil of Linnaeus came to England in 1760 and in 1765 was appointed assistant librarian of the British Museum. He went with Banks on Cook's first voyage (1768-71) and later became Banks' secretary and librarian.

and fair samples of rare and nondescript plants, so curiously and exactly extended and pre-
served and so many of them: and could not but wish that they might be drawn, engraven,
and published. But, alas! I find, as I told you, that I can make but poor work with them:
the fruit or seed scarce to be seen, at least perfectly discerned, in any of them: neither the color
or figure of the flower, without marring the specimens, which it were a great pity to do: the
stature to be known but in few, and nothing of the root. Those that gathered them might
easily have given an account of all these, as also of the place where they were found. For
my part, I am loth my work should want such an ornament, yet am I afraid to meddle with
them, having not been conversant among dried plants, especially Indian and American."

It would appear that Vernon's stay in Maryland was but short; we have no record of
his death, which occurred before 1716. He is commemorated by Schreber's genus *Vernonia*.

Rev. Hugh Jones (fl. 1697-1701) is described by Petiver as "A very curious person in all
parts of Natural History; particularly in fossils; some of which he later sent me from Mary-
land, with several volumes of plants very finely preserved; with divers Insects and Shells. From
this obliging gentleman I am promised frequent remittances of whatever those parts afford
as well Animals and fossils as vegetables". Mus. Petiver 44.

An account of animals and plants sent by Jones to Petiver from Maryland will be found
in "Phil. Trans. Roy. Soc." **20**:393-406. Fifty-six different plants are enumerated. The speci-
mens which are scattered through Petiver's "Hortus Siccus Americanus," (Herb. Sloane 157-
159) are apparently those referred to in the "Museum" "as presented to Petiver by Mr George,
London, his majesty's gardener" "two volumes of dry plants very curiously preserved, and col-
lected in Maryland by my worthy friend the Reverend Hugh Jones"—one, *Vaccinium stamin-
eum* L. (Herb. Sloane 159.f. 183) is labelled in Jones's hand "A huccle-berry with a white
blossome in Aprill".

His letter to Petiver, Doody and Ayry jointly, dated from Maryland March 26, 1697, gives
an account of his voyage and of his first impressions of Maryland where he had been appointed
"Minister of Christ Church parish in Calvert Country." A second letter (Feb. 26, 1701) mentions
that he has sent Petiver plants and seeds but that the state of his health has prevented him
from making as complete a collection as he had wished, and that he was thinking daily of a
return to England". His death seems to have taken place shortly afterwards in Maryland.

Archibald Stewart, a Surgeon (fl. 1699) sent ferns from Darien to Petiver (Museum no.
52); these are preserved in Petiver's "Hortus Siccus Americanus." The specimen of *Selaginella
flabellata L.* (Herb. Sloane vol. 157 f.8) bears one of Petiver's original tickets reproduced from
his 'Museum' no 533 p. 52) which reads,—"no. 533. *Muscus denticulatus Caledonicus major
perelegans. Filici in modum pinnatus.* This elegant plant, my worthy friend Mr Archibald
Steward, Surgeon, brought from the Scots settlement at Darien." On the same sheet is a
specimen from Dr. Barham from Jamaica with a label in Vaillant's handwriting.

James Wallace M. D., F. R. S. (fl. 1684-1724) also gave plants to Petiver from Darien which
are preserved in his "Hortus Siccus Americanus" (Herb. Sloane vol. 157). See Petiver
"Museum" m. 53.

In Phil. Trans. Royal Society **22**: p. 536. 1700 is a communication entitled—"Part of a
Journal kept from Scotland to New Caledonia in Darien with a short account of that country,"
communicated by Dr. Wallace, F. R. S.

The only reference to botany is the following: "This place affords legions of monstrous
plants, enough to confound all the methods of Botany ever hitherto thought upon. However
I found a shift to make some specimens and that is all I can do. . . . . Some of their leaves
exceed three ells in length and are very broad; besides these monsters, reduceable to no tribe,
there are here a great many of the European kindred (but still something odd about them) as
'Lingua cervina' of different kinds, *Filix* of different kinds, *Polypodium,* several of the *Plantae
Papilionaceae, Musci, Fungi, Convolvuli,* and a great many more I cannot remember."

Two other surgeons who sent or brought Petiver plants from Virginia were William Brown
(or Browne) "My late industrious friend Mr William Brown, Surgeon" (Petiver in Phil. Trans.
30:355. 1715) he also brought Petiver plants from Gibraltar and the Cape: and James Marshall

who brought 'plants and coral' to Petiver and Plukenet; numerous specimens, usually poor, are scattered through Petiver's American Herbarium (Herb. Sloane 158, 159) occasionally with autograph tickets.

Another correspondent of Petiver's was George Francklin (1700-05)—"My kind friend Mr George Francklin apothecary sent me some plants he observed the last spring about Charles Town in Carolina". (Mus. Petiver 80 [Dec. 1700]). Francklin was apparently in practice there and collected in April 1700 (Herb. Sloane 158. f. 92; see Mus. Petiver no. 744), but returned to England and lived at Downtown Wilts. Specimens with autograph labels occur in Herb. Sloane 158, 159. His letters to Petiver (with whom he seems to have been on friendly terms before leaving London) from Carolina (1700-1) relate to the sending of plants and other objects: in one (May 2, 1700) he speaks of having sent "a quire almost full of samples: some of them I know no name for, but some I have sent you both the name and the time and place of collection." On his voyage home for England his ship was taken by the French—apparently in 1703; but on Nov. 24, 1705, he writes to Petiver from Downtown, where he "had a little bussinesse".

Any reference on my part to John Bartram of Philadelphia (1699-1777) whose specimens are contained in three volumes of the Sloane Herbarium (332, 3, 4), as well as in considerable number in Herb. Banks, is unnecessary. His son William (1739-1823) is rather outside the period I have been considering, but I should be interested to know whether any of his specimens exist in Philadelphia. William Bartram sent specimens to Dr. John Fothergill (1720-80) (a London physician who practised in Lombard Street and was a correspondent of Linnaeus) which ultimately came into Banks' possession and are in part incorporated in Herb. Banks. We have in the Department of Botany at the British Museum six little quarto books of his plants. Books nos. 2 to 6 are variously labelled, "For Dr. Fothergill, London, specimens of plants from Georgia" (books 2 and 6) "South Carolina" (book 3) and "Eastern Florida" (books 4, 5).

The most interesting is, however, Book 1.—"Specimens of Trees, Shrubs and Plants collected in Carolina, Florida and Georgia 1773, 4, 5, 6 with notes and observations by William Bartram." It contains 38 specimens arranged according to the Linnean system, and partly determined specifically, with numerous very neatly written notes as to locality, characters, etc. The plants are referred to and some are figured and described in W. Bartram's "Travels through North and South Carolina, Georgia, E. and W. Florida," Philadelphia, 1791. No. 1 is *Franklinia alatamaha* W. Bartram, Travels Sp. 16, previously described by Marshall (*"Arbustum Americanum,"* Philadelphia 1785) a synonym of *Gordonia speciosa*. Descendants of the original tree planted by Bartram are, I believe, still growing in his old garden at Philadelphia.

Two other species are Nos. 22 and 23 labelled *Anona,* which are the *A. pygmaea* and *A. grandiflora* respectively of Bartram's "Travels" (p. 171). Both species are now placed under *Asimina*[3] but still bear Bartram's trivials. Neither of them is mentioned by Marshall.

At the end of the little book, which measures 10 x 8½ inches and is made of the mounting paper of the time sewn together, is an interesting account by Bartram of his collections; it is dated Nov. 1788.

John Lawson (d.1711) was Surgeon-General of North Carolina from September 1700 until his death, an account of which is given in a letter by Major Christopher Gale, Attorney General and Chief Justice of North Carolina, published in Nichols' "Illustrations" 4: 489. A rising of the Indians took place in September 1711, and on September 22nd, Lawson, who was on a "progress to the Indian towns" was murdered with his company: "they stuck him full of fine small splinters of torchwood like hoggs' bristles and so set them gradually in fire".

A very full account of the natural history is given in his book "A new voyage to Carolina containing the exact description and natural history of the country together with the Present State thereof and a journal of 1000 miles travel'd thro' several nations of Indians giving a particular account of their customs, manners, etc. By John Lawson, Gent. Surgeon-General of

[3] [See A. W. Exell in Jour. Bot. **65**: p. 65. 1927, A.B.R.]

North Carolina. London. Printed in the year 1709." Lawson started from Charleston Dec. 28, 1700 and pages 1-60 contain a diary of the journey. The section on the "Vegetables of Carolina," occupying pp. 89-115, describes the native plants and seeds with their uses and gives an account of 'what exotick Fruits thrive well in Carolina" with suggestions for planting. In a long and interesting letter to Petiver dated Dec. 30, 1710, he plans out a thorough investigation of the natural history of the region.

The book, which is rare, was reissued in London, 1714, with an altered title-page, "The History of Carolina, containing the Natural History."

Herb. Sloane vol. 145 (ff. 45-66) contains plants collected by Lawson in Carolina in 1710; and vol. 242 (ff. 110-136) trees and shrubs collected in Virginia in 1711; prefixed to the volume is a list of "Lawson's Virginia Trees" in Petiver's hand. Many of the plants bear autograph tickets, some signed, bearing notes on the specimens or indications of locality, often with reference to the page and line in the "New Voyage" where the plant is mentioned or described.

In Vol. 242, f. 121, is a specimen of *Carya alba* Nutt. collected at Salmon Creek, April 21, 1711 and described as "The hiccory with tassells, the nuts and not these are ye seeds", T. Lawson. A lower label reads "April 21, 1711. A smaller hiccory with tassells. N.B. Ye leaves may differ by a different age in ye tree. Yet I take these two to be different." Vol. 242 is smaller than the usual size of the Sloane volumes. In vol. 145 a number of specimens are mounted on each sheet. Folio 50 contains *Cypripedium hirsutum* Mill. (in fruit), *Taxodium distichum* Rich. "Bald Cypress pag. 96", *Smilacina racemosa* Desf., *Calopogon pulchellus* R. Br., and *Cyrilla racemiflora* L.

Folio 59 contains *Vaccinium arboreum* Marsh. with a label "Winter huckleberries not mentioned. You shall have the fruit when ripe wh is not till ye 8 br or Xbr. June 4, 1710." *Oxydendron arboreum* DC. "Sour wood tree, pag. 98 line 5^{me} Gott in Trent-River June 16, 1710." *Yucca filamentosa* L. "Silkgrass in flower. Trent Rv. June 8, 1710." Also *Castanea pumila* Mill. and others without original labels. One specimen is a 'composite' consisting of the inflorescence of *Cephalanthus occidentalis* L. (Rubiaceae), and a leaf of a species of *Vitis*.

Lawson's plants ran into hundreds and while many are unlabelled, quite a number are accompanied by tickets similar to those of which I have given examples.

The above instances will indicate that we have at the Museum collections which would repay examination by American botanists. In many cases the plants have never been determined, or have only the original reference to Ray's "Historia." But a botanist well acquainted with the American flora would have no difficulty in naming them and I would be delighted to give such an one every facility for the work.

THE DUAL PURPOSE MANUAL[1]

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The simple title just announced for this brief paper may seem to suggest a subject too trivial for consideration by the leaders of the Botanical World assembled in an International Congress. I must confess that I share in that feeling until I try to justify, in my own thinking, the existence and the persistence of taxonomic work in Botany or any other science.

That Taxonomy should have been the first phase of our subject to secure the standing of a science needs no explanation. We recognize that fact as merely the orderly development that inheres not only in this subject but in the normal development of man and of his mind. The problems of morphology, physiology, environment, and heredity do not present themselves until we *know* (please note I did not say know the *name* and the *classification*) the organism or group of organisms that claim our attention.

It seems quite possible that vigorous inquiring minds of past centuries may have grasped many of the truths of modern botany, but unless they were able to fasten their thoughts to the printed page by means of the nails of recognizable names their thoughts perished with them. Such thinking is amoeboid science, each generation starting at the same point, indulging in the same activity, but getting nowhere.

I do not wish to say, as others have said, that taxonomy is the fundamental phase of all the natural sciences but rather that it is complementary. To say that it is fundamental implies that it is something that might be finished like the foundation of a great building—dead concrete upon which shall rest dead stone and mortar, dead steel and glass, organized into a thing of beauty for us to admire until the ravages of time convert it into dust.

Man has always been more or less dependent upon the products of the forest, and there came a time when he devised and fashioned crude implements with which to secure and convert to his use these products. From these earliest implements to the modern machinery for lumbering and for the conversion of forest materials into products of use or beauty is a long evolutionary road. One does not think of this long line of successively changing implements and machinery as fundamental to our use and appreciation of the forest and its products, but rather as indispensable equipment that could not have been invented except as necessity for it arose in an advancing civilization. Just so, one does not think of plant names and schemes of classification as antedating the science of botany,

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[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 20, 1926.

but rather as the machinery which is gradually being perfected to the end that we may utilize more fully the products of our great field.

Symbolizing our study of life upon the earth as a tree, its base is the science of biology and its dichotomous trunk the sciences of botany and zoology. This symbolic tree not only *represents* living things but is itself a living, growing organism. Its various branches and branchlets are not independent of each other but coordinate and subordinate elements of a unified whole. Taxonomy is not a twig upon this tree. Classification in botany, along with its specialized vocabulary, is the fibro-vascular system that ramifies even into its leaves and fruits. Morphologists, physiologists, horticulturists, and all the rest of us could be in better business than making fun of ourselves. Our bodily organs might as well make fun of our skeletons. Circulation, respiration, and innervation occur in animal forms lacking an endo-skeleton but the work of the world does not rest upon those forms. Our botanical efforts are equally impotent in the absence of a satisfactory taxonomy.

Now I will admit that taxonomic systems are neither adequate nor infallible, but has any field of botany become static by reason of its complete development? Is not the fact that they are changing the best evidence of life in them? Even so with taxonomy. The "artificial system" of Linnaeus yielded to the "natural system," but the latter is still in the making. It cannot reach perfection until we have a perfected morphology. Our conclusions in morphology and physiology are often based upon our conception of their interaction upon each other and upon the effect of environment upon both. I am not enumerating these elemental, obvious facts for their own sakes but rather to emphasize the incompleteness of taxonomy and the extent to which it inter-locks with other fields.

In view of these things, is it not evident that all the workers in the great field of botany have a common interest in a simple classification, made available through a stable, usable nomenclature? We should by now have forgotten that taxonomy ever existed for its own sake alone. The dictum, "Science for science sake" is all well enough in its place but taxonomy for the sake of the taxonomer is another matter. In the periods of exploration, we are all fascinated by the novelties secured but when "the tumult and the shouting die" we must incorporate the results with what the world possessed before. The species maker with his analytical mind is much given to leaving that to constructive minds that can whip dismembered facts into a compendium for the use of his fellow workers in other fields or even for the educated layman.

Possibly some of the demands I make upon taxonomy seem inconsistent with each other—notably, that it shall be considered a living, growing science and therefore a gradually changing system, while at the same time I insist that the nomenclature shall be internationally stabilized. Scrutiny of these demands, however, reveals no inconsistency. The first deals with the arrangement of the facts of common knowledge and must necessarily change as further facts become our common property. A stable international nomenclature, however, makee possible a coordinated unified advance upon all the botanical frontiers of ths world. A gradually perfectable system of classification is impossible, it seems

to me, apart from a universal stable nomenclature. Whether the world be ready for international peace in the political world it is not my privilege to inquire, but certainly we have advanced far enough as scientists to proclaim complete amity in botanical affairs. The discussion of legislation by which nomenclature may be internationally stabilized has been barred from this session of this Congress but certainly no harm will result from the announcement of our unalterable adherence to that principle.

This lengthy introduction to so trivial a matter as the form which a Manual of Botany should take may seem ludicrous but for the fact that I am not much concerned with a given manual but rather with the objectives that should govern the authors and compilers of manuals. Because of the way I am developing this paper, it reminds me of the ancient Plesiosaur; its neck is longer than its body. Had it not been christened "The Dual Purpose Manual" before the paper was written, its title might have been different.

There is no word in the English language so universally used to convey a great idea as the word *Service*. There is no idea that has entered into the international mind so fully, in war and post-war days, as the idea conveyed by this word. The idea was given to the world by the Great Teacher more than nineteen hundred years ago. Consecrated teachers since that time have tried to illumine its meaning during the centuries as they have come and gone but only the idealists have caught its significance. To the average man it has only a spiritual meaning and that in a world that lies outside of his ken.

Somehow the Great War helped all the world to see that service was a practical idea and not merely a spiritual ideal. It became the aim of the individual and the slogan of the organization. We get service from our congressman and from our barber; from the government bureau and the filling station; from the church and the clubs. The business men's luncheon clubs, now organizing in all lands, express the hope that these organizations may successfully promote international peace through the spread of brotherly understanding and goodwill. May their hopes be more than realized.

The dual purpose Manual that I have in mind might be called the SERVICE MANUAL in Botany. To justify this name may I enumerate a few of the results that I hope might come from the type of manual that I have in mind.

1. The redevelopment of interest in botany among intelligent people everywhere. Our system of classification and our nomenclature have become so complicated that even an educated laity has been unable to follow. Other interests and pastimes—notably athletics, motoring and the movie—have bidden with insistent publicity for recognition. The results have been a deadening indifference to the charms of the living world and we as a people have lost the cultural value of a science that can do so much to promote that type of happiness that comes from a sympathetic contact with and an adequate understanding of that part of our environment that brings re-creation to our bodies, joy to our minds and peace to our souls—the world of life about us.

I wonder if the taxonomists themselves are not largely to blame for the indifference, the existence of which we all admit. Have we not largely assumed

the attitude of some of the great corporations of some decades since, namely, "The public be damned"; "Don't bother us, we are busy discovering, sub-dividing, and pigeonholing"; "When we are through with the scientific end of this, maybe we will tell you about it." The result has been that the public does let us severely alone. A novel, dashed off in six months, if it be hot with human interest, is snapped up by the first publisher to whom it is offered and makes a fortune for the house and a competence for the author. Our manuals that represent the explorations of many, the tedious comparison of thousands of specimens and the painstaking writing of descriptions, to say nothing of the "cross-word puzzle" type of ingenuity required to build the keys, go begging for a publisher. That it has cost years or decades, sometimes a consecrated life-time, and that it represents the best information available is nothing, and justly so, to the publishing house if the public does not want it. You who have put your own meager savings from an attenuated salary, almost the bread and butter from your tables, into the publication of your own lifework, rather than see it lost to the world, will understand. The public *will* pay for what it wants but we must find the key that unlocks the public's interest. If we can do that it will not be necessary to pursue a potential patron who has a plethoric purse with pleading petitions that he pile up ponderous tomes for posterity. The second-hand book-dealer of the next century, under present conditions, may be able to advertise as now—"clean," "uncut," "as new."

Do we not have another example of the necessity of sharing with the public our scientific results in the humiliating controversy in America concerning evolution? Crass ignorance on the part of the public as to the doctrine and the truths that the scientists actually teach is responsible for the stupid legislation effected and under consideration. The religion of an evolutionist is usually profounder and far more reverent and based upon a nobler conception of Deity than is possessed by his persecutor. The fundamentalist is one who reveres truth, but failing to recognize it in the garb in which the modernist presents it, he fears it, as established orthodoxy has always feared progress outside of its sphere of thinking. I am pleading, therefore, that in our scientific work (even in our manual making) we carry our results to the public in as simple and under-standable form as possible. Had biologists been consistently doing that there would have been no Scopes trial and manuals would still be a safe financial proposition for the publisher.

The next result that should come from the type of manual I have in mind is the re-establishment of taxonomy in the curricula of secondary schools and colleges. That, it seems to me, would do much to correct the conditions that have already been discussed. It would mean:

a. Trained sympathetic teachers for nature study classes.

b. Respect for the science by patrons of the schools.

c. Cooperation instead of censure from botanists who are working primarily in other fields.

d. Community of understanding among biologists.

 e. The development of interest, initiative, judgment, and common sense mong the youth of today.

 f. The enlistment of the interest of thousands of amateurs whose pleasures in the out-of-doors would be immeasurably enhanced.

 g. The enrichment of life and letters through a finer understanding and a keener appreciation of one's environment.

 Now I do not for a moment imagine that I have conceived a method in manual making that will popularize systematic botany. I am hoping, however, that a discussion of the needs may lead to thought on the part of others, the total outcome of which shall be a larger service.

 Systematists are relatively few as compared with the workers in other lines. In fact, those following taxonomy as a profession are so scarce that only rarely do we see one. In the main the work has to be done, now as in the past, by those who have won their standing in the world of science in lines other than systematic botany. Most of them are teachers, investigators or administrative officers, with taxonomy merely as their avocation. It is by these, drawn into the work by their love of it, that the great body of accumulating facts is being hammered into a usable system. Those who like myself merely dabble in Taxonomy as a side-line do so with fear and trembling, but all the while hoping that we may do more good than ill in the long run.

 One of the primary reasons for all taxonomic work is service to the workers in the other fields of botany. Money and time spent on it is not justified unless, in addition to "science for science's sake," the general user of works on Systematic Botany finds it easier *to know* the plants with which he is dealing.

 The basic principle underlying the manual of which I am thinking is *simplicity* from the standpoint of the user. This criterion, if taken as a guide will sometimes segregate and sometimes combine closely related families, genera and species. There is nothing sacred about the family and generic limitations, except as the boundaries of these affect that which should be more sacred than it is, namely, well known long established names. Binomial combinations, that have become the symbols by which certain plants enter into the thinking of the public and into the needs of workers in all the fields of botany and the allied subjects should not be changed except for reasons that can command international approval. The building of a "Service Manual" therefore involves simplification tempered with judgment.

 It should be remembered that what I am taking about does not concern the work of the specialist in his exploration or analysis of a floral district or the monographic study of a family or genus. These are tasks that are fundamental and antedate the compilation of manuals.

 Many plans for bringing the manual into popular favor in this and other lands have been tried. Simplicity has been sought during the last two or three decades through segregation of families and genera but those of us who have done so are finding that simplicity lies not in that direction. We had lost track of the fact that the first qualification in systematic work is the ability to see resemblances. The basis of classification is likeness. I think, therefore, we must return

to the sanity of an earlier generation and restore the larger unit, to be segregated within itself by the specialist for the specialist as fully as his needs demand and as his judgment justifies. For the "average user," if we would bring him back into our field of thinking, we must base our work upon the outstanding characters of primary species.

To this end I should like to see a manual constructed upon the following plan. I doubt if it would be workable for large geographic areas—certainly not for larger areas than that of the Gray Manual region. Preferably it should be tried out for an area no larger than that of the Coulter-Nelson Manual of the Central Rocky Mountains or on state floras. For such an area, limited and well defined, I offer the following condensed specifications for a one volume manual, in two parts:

Part I should be complete in itself. This part would contain the keys to all the families (all references to units are to be understood as referring to the area of that manual only) with concise but adequate descriptions. Synonyms, if any, to follow the family description. Then would come the sectional and generic keys. Then, in the usual manner, the generic treatment would follow. The generic description should be diagnostic but not elaborated. Synonyms should follow, and if it were a synthetic or rehabilitated genus, a statement should show clearly what fragments had been remanded to the original concept name.

Genera would be treated in one of the two following ways:

(a) Small genera, that is, those having only a few species (say for instance ten or fewer) would receive complete consideration. A key to the species would precede the specific descriptions. The names should appear with author and complete citation. The diagnoses should be condensed but the characters chosen should be such as to permit of direct comparison with the similar structures in the sister species. Synonyms, with citation, should be given in reasonable fullness, so that the critical student would have at least a starting point for further investigation. In the case of a rehabilitated genus, there would seem to be no adequate reason for using up costly space in reproducing all the combinations, with their citations, occasioned by its previous dismemberment.

(b) Large genera, that is, those having many species (say, for instance, more than ten) would have exactly similar treatment except that only a portion of the species would be included. Genera like *Astragalus* (you will see I am thinking of the Rocky Mountains), *Potentilla, Penstemon, Senecio*, and others, would receive double treatment. In Part I would appear only a selected representative list of generally accepted, widely distributed non-controversial species. The number to be included naturally would vary with the character of the genus and the distribution and significance of the species. Genera of that kind would have a simple key covering only those species chosen for inclusion in Part I.

Part II of the manual would appear as supplementary to Part I. In it would appear a complete synoptical treatment with keys, of all of the larger genera not fully treated in Part I. Page references in Part I would lead the user, without loss of time or continuity, to this fuller consideration. The species treated in Part I would be included in the complete keys to the species of a given genus.

These would not be redescribed but might be designated as of Part I by an asterisk.

To recapitulate: Part I would be complete in itself, serving all users, laymen and students. It would contain all general keys, leading to all families and genera in the area covered. In connection with each genus, there would be simple keys and adequate descriptions of all the species, if few; of the common representative species only in the larger genera. Since the bulkiness of manuals is largely due to the disproportionate space required for the treatment of a relatively few very large genera, the transfer of their complete treatment to Part II would make of Part I, when issued separately, a handy volume for the average user. The result, however, would be that every user of Part I would have before him the constantly recurring suggestion that he should possess the complete manual in order to see the full development of the genus in which he happens at the time to be interested, *Phlox* or *Oxytropis*, for instance.

Part II would not be issued separately. It would contain no family or generic diagnoses. It would be merely a succession of those genera in which, by reason of the number of species involved, a more critical analysis is required in the keys and more careful diagnoses of the species. The synonymy and citation will present more difficulties than in Part I. If it seems necessary to conserve space and keep down cost, a more or less synoptic treatment and smaller type might be adopted

To the critical student such a manual as here outlined would be indispensable as a starting point for further work in that field. These would, of course, require the complete manual since the publishers would issue the manual in two forms only—Part I by itself; Parts I and II together—never Part II by itself.

The plan as here outlined would, of course, be tentative and subject to such change as experience in actual construction would suggest.

SCYLLA OR CHARYBDIS[1]

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Botanical taxonomy in any country passes through three stages of development, depending upon how many plants are known and how well these are known: phytography, taxonomy in a limited sense, and phylogeny. When the flora is practically unknown, any attempt at a systematic treatise would be futile. The so-called taxonomic work naturally then is limited merely to descriptions of plant form. This kind of work should be called phytographic rather than taxonomic. The work of our earlier botanists, such as Walter, Michaux, Pursh, Nuttall, Eaton, and Woods fall mostly into this category. Even some of our more prominent taxonomic botanists of later years may be classified mainly as phytographers, as E. L. Greene.

Real systematic work in North America began we may say, with John Torrey. His "Cyperaceae" was indeed a remarkable work. After the death of this Nestor among American taxonomists, all monographic work among phanerogams was practically confined to Harvard University for about 40 years. After Gray's death, the younger generation began to dare dabble in systematic as well as descriptive botany. I will admit that phytographic work in the last 35 years has been overdone and I myself can scarcely plead "not guilty" to such a charge. One reason for this intensive work has been the active field work done, especially in the 1890's, with a host of new forms discovered.

In 1829 Amos Eaton stated, in the preface to his Manual, "There are not, probably, 50 undescribed species of phanergamous plants in the United States— perhaps not one species east of the Mississippi." In another place he supposed that perhaps 10 per cent of the species west of the Mississippi were still unknown. If he had said "known" instead of "unknown", he would have been nearer the truth. Even in 1890 I think that, with the exception of the northeastern quarter of the country, the flora of the United States was scarcely more than half known.

Another reason for so many new descriptions is that the authors in their eagerness often overlooked each other's work and that of their predecessors and descriptions were duplicated. A third reason, and this perhaps most applicable, is that the more the taxonomist studies a genus or a family, the more forms he recognizes, and the better he knows the family, the finer splitter he becomes. Then he either distinguishes more restricted genera, or recognizes infinitesimal species; or perhaps he recognizes large genera and broad species, but splits these into numerous subordinate categories: subgenera, sections, groups, subspecies, varieties, forms, etc., without end.

[1] Presented before the International Congress of Plant Sciences, Section of Taxonomy, Ithaca, New York, Aug. 20, 1926.

Very little work has been done in this country in the third stage of taxonomy. The only intensive work aiming to demonstrate phylogeny is the newly published "Phylogenetic Method in Taxonomy" by Hall and Clements. The fact that this is the only one is one of the reasons why I shall dwell so much on it and shall give it such predominance. I realize that it is bad taste to encumber a paper before this dignified audience with so much criticism of a single work, but it presents principles altogether different from my own and gives me excellent material for illustrating my contentions.

I cannot speak for all the taxonomists in this country, but only for myself and a few close friends, whose views I know. We have seen the endless and infinitesimal splitting into categories of the German school and for twenty years have been thoroughly disgusted with their absurd nomenclature of trinomials, quadrinomials, and polynomials. We believed that any form that is worth describing is worth a name and that a binomial is better than any other. But we might have forgotten that there is a Scylla as well as a Charybdis.

That the "endless" splitting of genera and species should meet objection especially among non-taxonomists was natural. These objections have been voiced in this country, at least in print, strongest by some of the leading ecologists. The objections might have been warranted, but they should not have been presented in an overbearing and sarcastic way. I felt strongly tempted to give them some of their own medicine. How can ecologists teach taxonomists the way to do their work? One of the former undertook such a thing and for the purpose roped in one of our best taxonomists to help him and the result was the publication of the "Phylogenetic Method." I admit that phylogeny is the highest stage of taxonomy and should be the climax of systematic work, but are we ready for that kind of work in this country? Time and money could have been better spent in monographs of groups. Hall himself had published some work on the smallest of the three genera treated, that is *Chrysothamnus,* and of the other two, *Artemisia* and *Atriplex,* rather exhaustive monographs had been published lately. If this paper was intended as a review of the publication, I would give a good deal of praise to the main part of it. The credit is due cheifly to Dr. Hall. It is the purpose and the principles laid down in the preface that I object to, and the inconsistency in carrying out the plan. The preface was evidently written principally by Clements. In trying to reform taxonomy they forgot that there is a Charybdis as well as a Scylla. The authors of the preface criticize "the tendency during the last two decades in America at least of segregating genera and raising their sections to generic rank." It is true that the splitting may have gone too far, that the school of taxonomists represented by my own institution has dared too near Scylla. Some may think that we are already shipwrecked. Judging from the printed text, the authors referred to seem to think so. Let me quote their own words (page 7) "Relationship and perspective are lost and the results are both unnatural and unusable. It is necessarily in the largest and best known genera that segregation has been rife, and it is these that offer the greatest opportunity for damage both to phylogeny and to classification. In North America, *Astragalus* is unique in

that it is now represented by 19 genera, so-called; *Aster* is segregated into 13," etc. "The 18 segregates of *Astragalus* are much more nearly related to each other than they are to *Robinia* or *Trifolium*, but there is no evidence of this fact in their treatment." The last statement is far from the truth. I happen to be the man guilty of the segregation. In my "Flora of the Rockies," the last publication in which the segregated genera appeared *Trifolium* is placed in a different tribe, and in the "North American Flora" (vol. 24, part 3) *Robinia* is placed in a different subtribe from *Astragalus*. But why select *Robinia* and *Trifolium?* Why not compare the segregates of *Astragalus* with genera generally recognized in the same subtribe, for instance, *Oxytropis, Gueldenstaedtia, Calophaca, Caragana,* or even with genera outside the subtribe but with more of the same general form as *Astragalus,* for instance, *Colutea, Cracca, Galega, Benthamantha, Peteria,* etc.? It only shows how little the author of the introduction knows about *Astragalus* and its segregates. If it had been written by Hall, one would expect more careful statements. If the time allotted to this paper would admit, I could easily show that *Phaca,* one of the segregates, is more closely related to *Colutea* than to *Astragalus* proper; that *Homalobus* and *Kentrophyta,* two other segregates, do not even have the characters assigned to the subtribe Astragalanæ by Bentham and Hooker in their "Genera" or by Taubert in the "Pflanzenfamilien", and that at least two of the species of *Hamosa,* also a segregate, have beaked keels, the diagnostic character of *Oxytropis. Astragalus* is not a natural genus as limited in the Pflanzenfamilien. It contains shrubs and herbs of various habit, with odd-pinnate or even-pinnate or even digitate leaves, with beaked, acute, or blunt keel, 2-celled, partly 2-celled, or strictly 1-celled pods, in texture from papery to woody, dehiscent or indehiscent, fleshy or dry, inflated or closely adherent to the seed, sessile or stipitate. There are no characters left to distinguish *Astragalus* from related genera, for instance from *Oxytropis* and *Colutea* while to the segregates one can assign characters which distinguish them from each other and from related accepted genera. This lumping, advocated by Hall and Clements has also been practiced by them. They include *Sphaeromeria* Nutt, *Vesicarpa* and *Chamartemisia* in *Tanacetum.* The only characters that Hall and Clements have left to separate *Tanacetum* and *Artemisia* are "Inflorescence cymose, the cyme occasionally reduced to a single head" in *Tanacetum* and "Inflorescence racemose-paniculate" in *Artemisia.* The inflorescence, strictly speaking, is neither cymose nor racemose-paniculate in either, for both have the flowers in heads. In my own treatise of the group I have used the word corymbiform instead of cymose, which I think is much better. Whether the heads are arranged cymosely or racemosely is hard to tell. If cymosely, the terminal or central head should be best and first developed. In such a case *Artemisia Pattersonii* should be included in *Tanacetum.* The heads of that species have exactly the same arrangement as in *Chamartemisia compacta* or *Sphaeromeria simplex,* that is, usually one or two heads, the terminal one the larger. Those two species are included in *Tanacetum* by Hall and Clements. If the heads are congregated into a spherical cluster as in *Artemisia glomerata* and *A. globularia* and *Sphaeromeria capitata* (according to

Hall and Clements a *Tanacetum*), it would be hard for any one to tell whether the heads are arranged cymosely or racemosely. In *Vesicarpa potentilloides* (also a *Tanacetum*) I can not tell if the inflorescence is racemose or cymose and I have dabbled in taxonomy for 50 years.[2] Is a vegetative habit of that kind a criterion on which one can build genera, wholly ignoring the anther-tips, the presence or absence of pappus, the different kinds of pappus, the presence or absence of a ligule in the marginal pistillate flowers, characters which have always been regarded as very important in generic segregation among the composites? Here Hall and Clements have used a supposed or trifling vegetative habit in the inflorescence as of great importance, but in *Chrysothamnus* the presence of resinous glands in the terete foliage of *Bigelovia paniculata* and *B. teretifolia* counts as naught, a character which in some cases has been regarded as important enough to distinguish tribes or even families.

When one of our taxonomists from the Pacific Coast (one of the conservative school) visited New York some years ago, she criticized Small severely for splitting up *Pinus* into four genera. "They are all pines," she said. Yes, unfortunately the English name is applied to all, probably because in England only one genus is represented by native species, that is, *Pinus* proper. In Germany, Italy, and France, the other genera, if represented, have different common names. In America botanists admit *Tsuga* as a good genus; it is here known (though erroneusly so) as hemlock, and therefore deserves generic rank, distinct from *Picea,* the spruces. *Tsuga* differs less from *Picea* than do the segregates of *Pinus* from each other. "If we admit *Tsuga* as distinct from *Picea,*" I said, "we have to admit *Apinus, Strobus,* and *Caryopitys,* if we are consistent." "Oh! darn consistency," interrupted the lady. That's it, "Darn consistency," that is what the crowd wants. That is really what Clements and Hall want. Lump genera together when Linnaeus, Bentham, or Gray has done so, split if the same authors have done so. Retain *Chamartemisia compacta* in *Tanacetum,* where the original describer, in this case Hall himself, had placed it, even if it is nearer to *Artemisia.* No, we want to go back to the *Linnaean concept of genera,* is Clements' statement. What was Linnaeus's concept of a genus? In some cases, he was exceedingly "conservative," in others what we would now call "very radical." He included *Castalia, Nymphaea,* and *Nelumbo* in one genus. The last one is now regarded as belonging to a distinct family, or at least a distinct tribe. On the other hand, he distinguished *Orobus* and *Vicia* from *Lathyrus.* The first differs from *Lathyrus* only in the absence of tendrils and the name is now generally discarded. *Lathyrus* is supposed to have the tip of the style pubescent above, glabrous beneath, *Vicia* the reverse,

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[2] I may here add that Mr. Wodehouse, a postgraduate at Columbia working for his Doctor's degree, has taken up the importance of the structure of the pollen grains in relation to classification of the spermatophytes. He has found that *Tanacetum* proper has the characteristic spiny pollen grains of the composites in general, but that in *Artemisia* the grains are perfectly smooth; so are they also in *Sphaeromeria* and *Chamartemisia* (both included by Hall and Clements in *Tanacetum*), which evidently strengthens my contention that they should be excluded from *Tanacetum.* In *Vesicarpa,* which Gray first included in *Artemisia,* later in *Tanacetum,* the pollen grains are different from both, being finely muricate.

or pubescent on both sides, characters exceedingly unreliable and omitted by Taubert from his key in the Pflanzenfamilien. He used instead "staminal sheath truncate at the apex in *Lathyrus*, and oblique in *Vicia*," a difference exceedingly hard to see in some cases.

The most weighty criticism of the New American school of taxonomists that their opponents can present is that it has produced a host of new names by splitting old genera. The constant change in nomeclature is not popular among botanists outside of the taxonomists, because it leads to trouble in ascertaining what name should be applied. It is hard to place an old friend when he appears under an entirely new name. Should we retain the old names and the old concepts, even if we have to sacrifice our own convictions? Yes, follow the crowd. Do as others have done before you. Split *Vicia* from *Lathyrus* on trifling characters. Linnaeus did it and he was a great botanist. Lump *Phaca* with *Astragalus*. Linnaeus established both, but he does not count. Ignore Medicus, who segregated into genera the then known European species on reasonable grounds, and Nuttall, who segregated two American genera which were accepted by Torrey and Gray. Follow Bunge, who knew the fruits of scarcely half of the species he treated, who wrote an elaborate but premature monograph, basing some of his main divisions on the structure of the hairs, a "hair-splitting" monograph indeed! He united *Astragalus* and *Phaca* of Linnaeus, throwing in *Tragacantha* (Tournf.) Miller to boot. But don't touch *Oxytropis*. It has no character which is not found in some one or another of the *Astragalus* segregates, but it was made by DeCandolle and accepted by Bunge, by Bentham and Hooker, by Gray, Watson, and Taubert. Is this consistency? No, but darn consistency! It is not popular, it is not conservative, it is not convenient. How is that; not convenient? I would like to see a real modern monograph of the *Astragalus* species of the world with between 1,500 and 2,000 species now known, about 500 of these in North America. Is it very convenient to keep track of such a host of names? Could it be written so as to show relationship and phylogeny without segregating it into 20 subgenera in America and not more than 30 in the whole world? Would it not be easier to remember the species and at the same time know exactly the relationship without going to the monograph? Would it not be better if these subgenera were called genera instead, that is, if 150 of these American species were called *Phaca*, 50 *Homalobus*, etc., reducing the true Astragali in North America to about 40? It is true that it changes nomenclature for the present, but would it not be more convenient in the future? It would cause some temporary inconvenience in America to change our measures to the metric system, but once done would it not be better? When the change was made in Sweden, there were not half the troubles that were anticipated. M. E. Jones once claimed that I had advocated that a genus should not contain more than 6 species. I have made no such statement. I have for years believed that large genera should be split up, if it can be done on scientific grounds. I know that this cannot always be done; for instance, two of the largest genera in the world, *Carex* and *Senecio*, are very natural as they are, though some fringes of the latter might be chopped off.

Ever since scientists ceased to believe in a special creation of each species, the old idea of distinct species has gradually become dimmer and dimmer, and I begin to think that there is no such thing except in our minds, and that the concept is different in different minds. The multitudinous forms we see are connected more or less everywhere by intermediate forms, and it is, in the majority of cases, almost impossible to draw a line between species, varieties, mutants, forms, and monstrosities. Where can we draw the lines? Prof. Cockerell once said that there are three kinds of species. In some genera the species are well defined, without any intergrading forms. In such a genus the species may be represented by large dots well separated. Here "lumpers" and "splitters" agree, they call all the dots species. In other genera the species can be arranged in groups, in which the groups are well defined without intermediates between the group, but with all kinds of intergradations within the groups themselves. Such a genus can be represented by a number of small dots placed in smaller or larger groups. Here botanists disagree. The "lumper" calls a whole group a species; the "splitter," each dot a species. In the third class there are intergradations everywhere, and such a genus may be represented by lots of small dots placed helter-skelter, without grouping. Here the botanists agree to disagree. No two botanists will have the same concept. In many genera all three classes are represented, as in *Artemisia*. The first class is represented by such species as *A. filifolia, A. stelleriana, A. rigida,* and *A. pygmaea;* the third by *A. vulgaris* and its relatives. In a genus of the first class there is clear sailing and both "lumpers" and "splitters" can keep the main channel, but in a genus of the third class the splitter is liable to be shipwrecked on the rocks of Scylla, and be grabbed by the 6-headed monster; while the lumper may be drawn into the everlasting whirlpool of Charybdis, where it is impossible to entangle the mass. Compare, for instance, the treatment by Hall and Clements of *Artemisia vulgaris* with its 15 subspecies and 99 minor variations or synonyms. Will posterity ever adopt all these forms as one species? On the other hand, I admit frankly that I have described in my revision as species a few forms that should rather be regarded as mutants, and a few others in which the material was too meager for a good description, but there is some definite system in my "insanity." Until the flora of a country is perfectly known, all forms existing should be described. This will help future taxonomists in placing them in the system. I fully agree with one statement in the introduction to the ''Phylogenetic method'' that "evolutionary taxonomy must regard the segregates of the last 25 years chiefly in the light of tentative proposals as to the course of evolution." Until we have discovered and described all, or most, of the great number of yet unknown forms, and until the species have been tested by cultivation, breeding, changing of soil and environment, etc., they naturally have to remain tentative. I leave it to others to find out whether the characters, prominent or trifling as they may be, on which they are based, are constant enough to place them as distinct species. I think that I have done a service to taxonomy if I have pointed out existing characters. I also think that a form that is worth describing, also should have a name. I prefer a binomial. When I use a binomial I do not pre-

tend that it means the same as a species in Hall-Clements style. I do not pretend to be able to pass on its rank, because in most cases it is impossible. A large percentage of the plants of any region is too little known for that purpose. When I find that a fellow botanist has described a species I try to maintain it, unless I find that it is a pure synonym or a freak. It shows more regard for other botanists' work, than does the Hall-Clements wholesale reduction of species, the species proposed by better botanists, for instance, Gray or Nuttall. It is not a craze for species-making, nor yet for attaching my name to a plant name that induces me to propose new species. I have already admitted that many of the new species should be regarded as tentative and should be tested. There are none who have a better chance to do the testing than ecologists and horticulturists—at experiment stations and botanical gradens. I agree fully with the author of the "introduction" in this respect, but when he begins in his discussion to elaborate on methods, work done, and results, it seems to me that the actual experiments and field work done had not been as great as these elaborations tried to indicate.

The author of the "introduction" states, "when definite ecological investigation was begun in the Rocky Mountains in 1899 much enthusiasm was felt for the recently segregated units." . . . . "Gradually it became evident that the so-called new species were herbarium-made and could not be expected to fit the facts in the field." . . . . "As a consequence of this attempt to make use of segregates, it was realized that the ecologist could work only with more objective units, checked with statistics and experiments [How many were tested?] and based on the fullest degree of evolutionary relationship. The outcome was 'Rocky Mountain Flowers' (Clements and Clements, 1913) in which a definite endeavor was made to relate the myriad forms to definite specific stock." Then he gives two tables comparing the numbers of genera, species, and varieties found in 4 books on the Rocky Mountain flora: Coulter's manual, of 1885; Coulter and Nelson, of 1909; Rydberg, of 1917; and Clements and Clements, of 1913. He prides himself on having reduced the number given even in Coulter's manual published 28 years before, when the flora of the region was not half known. In my opinion "Rocky Mountain Flowers" by Clements and Clements should not have been pointed out as an example of how taxonomists are to be taught to do their work. The illustrations by Mrs. Clements are fine, and I wish we had more of that kind, but the text is inferior.

One of the authors of the "Phylogenetic Method" claimed some years ago that the validity of certain species related to *Vagnera stellata* had been disproven by experiment; for when plants with conduplicate leaves from the open sunlight were transferred to shade they bore flat leaves; and those transferred from shade to sunlight changed in the opposite direction. Any taxonomist with some experience would believe this, but did it disprove the validity of these species? It is fair to state that in the official report the experimenters expressed the same thing more moderately, thus: "These have characters that have been used in taxonomic keys for the separation of supposedly distinct species." I may say, however, that they were not used by the authors in the original descriptions nor used in my "Flora

of the Rocky Mountains." Who knows? Perhaps only one and the same species was used in both experiments.

What experiments have the authors made to substantiate their reduction of three-fourth or four-fifths of the recently admitted species of *Artemisia and Atriplex?* They do not state in the "introduction." They say that they have spent five summers studying the three genera in the field, but the work was taxonomic, phyto-geographic, and generally ecologic. Did they do any experimental work that disproved the validity of specific rank? Many of the reduced species are shrubs, and no valuable results could be had by growing them from seeds in five years. As far as I can see, this wholesale reduction was merely guesswork, or an expression of their concept of species; and the boasting about improved methods mostly evaporation.

Some ecologists are very prone to take credit to themselves and to condemn the work of taxonomists. One of our leading ecologists (see Am. Nat. 42:265-271) states: "A little more and the sinning taxonomist will be cast out into the outer darkness where there shall be wailing and gnashing of teeth," and on another page: "One of the noblest aims of ecology is the destruction of many of the species of our manuals." If he had stated that the aim should be to find out the truth, even if it should cause the destruction of many of the species, I would subscribe to it. Unfortunately, he gives *Polygonum amphibium* and *P. Hartwrightii* as examples and he cites the classic experiment of Bonnier (an ecologist). Bonnier's experiment was done on *P. amphibium* and the variety *terrestre* of Europe, both known and named by Linnaeus, and it had nothing to do with *P. Hartwrightii*. *P. amphibium* is not found in America. Dr. Gray, who had a tendency to unite species, included *P. fluitans* Eat. in *P. amphibium* L. and most botanists have followed him. I think that most taxonomists will admit at least three amphibious species in eastern United States, some splitters would admit eight or nine not counting Greene and Niewland, who counted them by the dozen. The first species recognized as distinct was *P. coccineum* Muhl., with its variety *terrestre* of Muhlenberg, the latter form being *P. Muhlenbergii* S. Wats. The second is *P. fluitans* Eaton based on the aquatic facies, and *P. Hartwrightii* on the terrestrial. The honor goes to Bissel for discovering their identity. The third, *Persicaria mesochora* Greene, was described from the aquatic facies, the terrestrial being identified by Niewland. The identity of the two ecologic facies of these amphibium species was recorded by Linnaeus in 1753, Muhlenberg in 1813, Bissel in 1902, and Niewland in 1911—all taxonomists. Where did the ecologist come in? It is easy to make assertions without taking the trouble to verify the statements.

The author of the introduction to the "Phylogenetic Method" claims that we should return to the *concept of species of Linnaeus.* Who can tell what Linnaeus's concept really was and what it would have been if he had lived now with the hundred-fold forms now known? Linnaeus sometimes included in one species forms which now belong to different genera and even families, and in other cases recognized as different species forms which even the extreme splitter of today hesitates to distinguish; as, for instance, *Ambrosia artemisiifolia* and *A. elatior.*

He states further: "It is imperative to reestablish species on the basis of the traditional concept as exemplified in America by Gray and those that have worked in similar manner." How have the authors applied this theory in their own work? I felt very much hurt when I found that about half of the species admitted in my monographs in the "North American Flora" had been reduced to subspecies or varieties; then I tried to find out how they had treated Dr. Gray, and I felt much better. In the "Synoptical Flora" Gray admitted 46 species of *Artemisia,* of which 4 are introduced, leaving 42 native species. Of these the authors have reduced to subspecies or varieties not less than 21, or exactly one-half of Gray's species.

Does the Hall and Clements monograph then represent Gray's concept of species? I may have been seized by the monster Scylla, but did Hall and Clements steer the middle passage? Surely they were drawn into the whirlpool of Charybdis. One of the poorest of Gray's species, *Artemisia Pattersonii,* is admitted as a good species, probably because it is common on Pikes Peak, together with *A. scopulorum,* and is well known to both Hall and Clements in the field. Anyone that has visited Yellowstone Park would have admitted that *A. tripartita* and *A. nova* (reduced to subspecies) are fully as distinct from *A. tridentata* as is *A. cana* (admitted by Hall and Clements). Were they consistent? No. Darn consistency. Their reduction has gone to the extreme in the *A. vulgaris* group, where not less than 15 subspecies and 99 minor variations and synonyms are given. Is this wholesale slaughtering of species warranted? This includes species described by Besser (the best monographer of the genus for the World), Nuttall, Gray, Torrey, Greene, Nelson, Piper, Sheldon, Osterhout, Scheele, Douglas, Urban, and by me.

If Hall and Clements had raised to specific rank all of their subspecies in *Artemisia,* they would have had about the same species concept as Dr. Gray. The number admitted would naturally have been increased, but a great number of forms were unknown to Dr. Gray. If they had done so, they would have been more conservative, more consistent, and less liable to criticism. No criticism would have come to them from me, notwithstanding the fact that still quite a number of species admitted by me would have been reduced. The phylogeny could have been shown just as well.

Let us see how they have treated *Atriplex,* recently also revised in the "North American Flora," by Standley. Of course, they have reduced the number of species—from 103 to 47—but Standley is also a splitter. Did they keep the main channel in this case? Everybody admits that Watson was conservative and held about the same concept of species as Gray, yet more than one-half of his species are reduced by Hall and Clements. *Chrysothamnus* has not been revised in later years; so let us compare their treatment of it with Dr. Gray's. They reduced 8 out of 18 species admitted in the "Synoptical Flora." Is that a Grayan concept of species? They have 20 subspecies under *Chrysothamnus nauseosus,* where Gray had only 5 varieties. Is that not splitting for you? Does it not indicate that we all want to do as we please?

But Hall and Clements with their 20 subspecies are beaten by a German. Any one that tries to monograph one of the larger genera of Cockerell's third class

has a real "job" on his hands. Turn, for instance, to Zahn's revision of *Hieracium* in "Pflanzenreich." He admitted 756 species. If one studies his treatment of our American species, especially those of our west coast, one may regard him as a splitter, for he admits more species than any one in this country has done. Of these he admits no subspecies and few varieties. When the forms found in Europe are treated, he split up the species in several different categories. Would any one have expected him to split, for example, *Hieracium levigatum* into 4 greges, 7 sub-greges, 210 subspecies, and numerous varieties; and that our *Hieracium canadense* Michx. should appear as *H. levigatum* subspecies no. 195 *canadense?* Never-theless, he does not make a new combination, for he defines *H. canadense,* as well as the other subspecies, by a binomial name, which is so indicated in the index.

One thing pleases me considerably. Hall and Clements have not described or named any new species in *Atriplex* and *Artemisia,* or for that matter any subspecies, except as they have also burdened the nomenclature with the words "subspecies *typica*" in numerous places. That they could not find any new form worth a name is a most flattering compliment to the thorough work of Standley and myself. There is another redeeming feature of their work. They stopped, as far as real treatment is concerned, with the subspecies. If they had taken up varieties, forms, etc., in the main part of the monograph, there would have been a good many new quadrinomial and polynomials to burden the nomenclature. I am afraid that since they have beaconed the way, others will follow in their wake (Charybdis is very attractive) and we will soon have some Americans who adopt the fashion of some Germans. In "Pflanzenreich" we find an American plant under the name *Saxifraga tridactylites,* subsp. *adscendens* var. *normalis* f. *americana.* Small simply regarded the plant as the same as the European *S. adscendens* L. Nelson thought it different, and he adopted the name *S. oregonensis* (Raf.) Nels. The Splitters' ways are much to be preferred and will be adopted by the public rather than the quadri-nomial. Small followed the "concept of species" of Linnaeus, not that of Engler. *Artemisia arbuscula* Nutt. was the concept of Nuttall, Torrey and Gray, Gray, and myself, not *A. tridentata arbuscula* (Nutt.), Hall and Clements. We are satisfied with John Smith as a name. It is true that in Sweden a hundred years ago the common people did not have any family name and a boy was known as John Eriksson, but who would call anyone Joseph, son of Jacob, son of Isaac, son of Abraham, son of Terah, etc., just to indicate his pedigree or phylogeny? In Engler's name cited above half of the categories used by the same school were excluded, as subvariety, subforma, proles, lusus, mutans, etc. Who can distinguish between all these categories? I dare say not even the authors themselves. Graeb-ner in one place subordinated proles under variety as *Potamogeton pectinatus* var. α *vulgaris* proles 2 *interruptus;* but in another place he gave *Typha angustifolia* proles δ *Brownii* the same rank as *T. angustifolia* var. α *vulgaris.* Would not the average botanist, the amateur, the horticulturist, the physiologist prefer *Potamo-geton pectinatus* and *P. interruptus,* or *Typha angustifolia* and *T. Brownii,* to those Graebnerian names? Perhaps even ecologists would do so.

Ascherson and Graebner in their "Synopsis der mittel europäischen Flora" also

use polynomials. I could find no place in which they really indicate the categories, but their rank is indicated by numerals and letters. We find such pre-Linnean names as *Rosa canina glaucescens Touranginiana fallens* and *Rosa gallica erostyla pumila ruralis*.

Taxonomists of the splitting school have been accused of describing new species or splitting up genera for the purpose of getting their names suffixed to specific names. There is a much easier way to gain the same object. Reduce the species of other persons to subspecies or varieties by the wholesale! It is a comparatively easier thing to go over a fairly exhaustive revision of *Atriplex* or *Artemisia* and point out blunders than to segregate the forms originally. Reduce all species you can and write for instance *Artemisia vulgaris ludoviciana* (Nuttall) Hall and Clements [the trinomial meaning subspecies], when the plant already had the same trinomial, namely *Artemisia vulgaris* [var.] *ludoviciana* (Nuttall) Kuntze: is this not the worst kind of juggling with nomenclature? As a rule a trinomial has meant a variety in Gray's sense. It is true that some American botanists (for instance, Britton), have used the word subspecies instead of variety. If so used, Hall and Clements would not appear outside the parenthesis, instead of Kuntze. You may say, Hall and Clements have assigned a new rank. Yes, but they departed from the prevaling custom when using mere trinomials for subspecies. In Europe either the word subspecies has been inserted or else a binomial is used, often preceded by an asterisk.

In the "Phylogenetic Method" a trinomial means a *subspecies*, in "Herbaria formationum coloradensium" it means a *form*, as in *Polemonium pulchellum coryphocolum* Clements, a name used for the dwarf form of *P. delicatum* Rybd. Oh, consistency! It is not fair for me to make this comparison, for Clements, as well as any other botanist, had a right to change his views in 20 years. But his main argument has been that taxonomists of the school to which I belong have committed a great harm in upsetting the nomenclature and in the inauguration of an endless and useless splitting of genera and species. What has he done? He has inaugurated an entirely new nomenclature in ecology, very ingenious I admit, but at the same time it is not right for him to condemn innovations and splitting in taxonomy, when he himself does the same in ecology. He may answer: "My nomenclature in ecology is meant for experts, but the nomenclature in taxonomy is for amateurs, florists, foresters, farmers, for everybody." All right. Is not *Saxifraga oregonensis* or S. *ascendens* better for this purpose than *Saxifraga tridactylites adscendens normalis americana*, the result of the *Phylogenetic method*, if carried out? The fact is, Hall and Clements did not dare to carry it out. American taxonomists and amateurs also would not have stood it.

Another cause for changes in nomenclature is the transfer of species from one genus to another. This is also often dependent upon the different concepts of botanists, but perhaps more often due to the imperfect knowledge of the plant, or real errors committed by the original author. In the latter cases there should be no objections to the changing of the name. The third reason for changes are differences of opinions in nomenclature itself, depending upon a different starting-

point, a different concept of what constitutes a publication, priority of time and place, etc.

Only a few Americans have gone back of Linneus as a starting-point of nomenclature. Greene, influenced by Kuntze and Bubani, for some time advocated an earlier starting-point, but soon gave up this idea. Niewland and Lunell later took it up and have burdened our nomenclature with numerous unnecessary and in many cases unwarranted synonyms, even under the rules which they followed. Fortunately, hardly any taxonomist would be inclined to rescue these names from Charybdis. Most of the older systematists used whatever names they pleased. De Candolle was perhaps the first great champion for stability in nomenclature. Bentham and Hooker used as generic names mostly those that had been in general use, regardless of priority, and they were mostly followed by Gray, Watson, etc. Nomenclature took upon itself another face with the appearance of Otto Kuntze's "Revisio Generum" in 1891. He was a great champion for priority of names, and he found many followers in America. The result was the adoption of the Rochester Code, based principally on priority and the concept of types for genera and species. It seemed so feasible thus to produce stability. Its application, however, showed that it would lead into absurdities, partly because instances appeared which had not been foreseen, partly because those who applied it saw with Kuntze's eyes and relied upon his statements. He went back of Linnaeus in priority and claimed in numerous cases that certain names were published in certain years, when they were not published at all, or else many years later. The strict priority idea fell into disrepute, and at the Congress at Vienna a large list of *nomina conservanda* was adopted. To avoid the rocks of Scylla on which the Rochester Code was doomed to suffer shipwreck, the Congress threw its code in the whirlpool of Charybdis, the list of *nomina conservanda*. Such a list is not itself objectionable to me and to many taxonomists of the American Code, but the size of this list and the way it was made up are. It seems to me that it was made partly in order to save the nomenclature of Engler and Prantl's "Pflanzenfamilien." Many of the names included in it are superfluous, especially if the changes in the code to be proposed at the next meeting are adopted; some should not be there at all; and many are very arbitrarily selected, for instance, those of Salisbury, half of which were accepted and half rejected, although equally well published. This latter matters little, however, for I am afraid that "Do as you please" is the slogan. This list of *nomina conservanda* can be added and modified at the whim of any congress and thus it defeats any outlook towards stability.

The navigation through the botanical Straight of Messina is exceedingly hard. If a taxonomist tries to base his generic concept on distinct technical characters and believes that a genus should include only *closely* related species, or tries to be consistent, basing genera in the same family on equivalent character, he is an unpopular splitter. He upsets the nomenclature, adds numerous new names to remember. What is in a name anyhow? Let us know a plant by the name we are used to. If he tries to be conservative, he will probably be popular, but will he be consistent or even scientific? He has to resort to such artificial characters as

those that distinguish *Tanacetum* from *Artemisia* (unscientific on account of lumping done by Bentham and Hooker and by Gray), or *Orobus* and *Vicia* from *Lathyrus* (unscientific on account of too much splitting by Linnaeus).

If he believes that every form that is worth describing should have a name and that a binomial name, if possible, is preferable to a trinomial, quadrinomial, or a polynomial, he is again a splitter. It is ridiculous that *Artemisia* should have 120 species in North America as admitted by Rydberg, or Atriplex 103, admitted by Standley. Who can keep track of all these species? The number in the work of Hall and Clements is more resonable, 29 Artemisias and 47 Atriplexes. But is it? Is it more scientific? I doubt it. Is it more conservative? Hall and Clements reduce about half of Gray's and Watson's species, and their admitted species are fully as uneven.

If a taxonomist meets a genus of the first of Cockerell's classes, the sailing is clear and it is easy to keep the main channel. If he meets the second class, he has his choice, either to regard the individual forms as species (if he is a splitter), or as subspecies (if he is a lumper). If he meets the third class he is lost. There is no hope for him. The better he knows the genus the worse will he be off, the worse splitter he will become. Either he will make his species infinitesimally small (I am afraid I am inclined that way) or else he will make them unreasonably large, as Hall and Clements, and then go on splitting into subspecies, varieties, subvarieties, *ad infinitum*, as Graebner or Engler have done.

If he in his nomenclature believes in absolute priority, he runs into such absurdities as Otto Kuntze, Greene, and Niewland did; if he does not he is called unfair to his predecessors and is said not to give proper credit to the original discoverer or inventor, whatever he is to be called. If by publication he means simply a diagnosis, he has to adopt many of Adanson's, Necker's or Rafinesque's genera, poorly described and almost impossible to interpret; if he only requires a type, or type species, he adopts a very questionable name, as, for instance, *Jacksonia* Raf. based on *Cleome dodecandra*. Some botanists claim that this meant *C. dodecandra* L., others that it meant that species as interpreted by Michaux. Both diagnosis and type are necessary. How can a navigator sail with charts but no compass, or *vice versa?* If he objects to any list of *genera conservanda*, he is forced to adopt many genera which have a poor excuse for their existence and are based on absurd characters, for instance, *Aragallus* Necker. If he follows the Vienna Code, he is not better off, as the list adopted is arbitrary and inconsistent. If he is conservative and adopts a name in common use, he is accused of not being fair, if he is radical and does not, he is unpopular and upsets the nomenclature.

For years I have admitted that I am a splitter, but I have prided myself on being consistent, as, for instance, in splitting some genera so as to make them equivalent to other genera in the same family or tribe, but I have just discovered that in order to save already described species of other botanists, even if they have a meager excuse for their existence, I have added some of my own of the same category and made my species concept very inconsistent. I am inclined now to subscribe to the slogan "Darn Consistency."

COMMENTS ON THE SPLITTING OF GENERA[1]

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Many years ago while I was working with the small family Myzodendraceae for Engler's "Pflanzenreich," I was confronted with the question: splitting or not? Van Tieghem, who was a prominent splitter, had segregated some genera from the old genus *Myzodendron* of De Candolle which used to form the whole family. I soon found that, if I chose to follow the former, still another new genus had to be made. The characters used to distinguish these genera appear combined in various ways, and if I kept *Myzodendron* in the old sense, it still remained a very natural genus. I kept it. Later, when I tried to monograph the Juan Fernandez flora, I had to face the same problem. As an example, I shall give the key to the Composite genus *Dendroseris:*

Heads fairly large, flowers orange, achenes winged, leaves entire. Stem branched,
  hollow ....Subg. Eudendroseris
Heads smaller, flowers creamy white, achenes not winged.
  Leaves pinnate; stem unbranched, hollow ....Subg. Phoenicoseris
  Leaves entire; stem branching, solid ....Subg. Rea.

One of the species in the subg. Rea, otherwise quite typical, has the ligules split almost to their base, while in all other species of *Dendroseris* they look exactly like ordinary ligules. Ought I to make two, three, or four genera, or was it not better to keep *Dendroseris* in the old sense? Indeed, such genera would have been quite as good as many others. But when I found that nothing, absolutely nothing, was to be gained by splitting, I was able to resist the temptation. The same question turned up in another of the peculiar endemic genera, *Robinsonia*. Here the type species differs from all the rest in certain characters of the achene and pappus, and those other species form a couple of natural groups. This was indeed no discovery of mine, as sections had already been established by De Candolle. I found it necessary to rearrange his sections and to recognize subgenera, but I did not divide the genus. It might have been done, but the advantage of so doing I failed to discover. And I hope that both genera, and many more, will be allowed to remain as they are, although I know that if one of these latter-day splitters happens to cast his eye upon them, he will raise my subgenera or sections, having the great satisfaction not only of putting my initials between the degrading brackets but also of increasing the number of endemic Fernandezine genera to such an extent that few insular floras will show anything like it. Then it is far from true

that only large genera are attacked, the splitter who has got the right spirit in him does not despise to exploit the smaller ones .

The idea of segregation in all cases where there is a chance to do so is not an American idea, only, it seems to enjoy a higher reputation over here than it does in Europe at present. Lots of weak genera established by older European botanists are summoned from their graves and polished up again, and new combinations and changes of names follow in their wake. In my humble opinion, the situation has already become somewhat alarming. For this is not an American affair, it concerns everybody working with the Boreal floras. A host of genera and a great number of species belong to us as well as to you, but nevertheless we have to call them by entirely different names. This is certainly a good example of international misunderstanding. It has gone so far that many of us over in Europe are more than pleased for every genus that has not got any American representatives and is thus, at least for some time, left in peace.

If it was a question only of right and wrong, of logical, or illogical thinking, matters would, of course, be much more simple. But we cannot say that the splitter is wrong because he splits the genus *Pinus*, nor that his adversary is wrong when he refuses to do so, but the former shows bad taste and takes an altogether undesirable and unnecessary action, and that is quite bad enough when it comes to science. The segregation party advances the idea that the path it follows leads to greater clearness and accuracy. I shall try to show that this is a mistake.

In his paper this morning, called "Scylla and Charybdis," Dr. Rydberg, who certainly knows more about taxonomy in this country than most other people, threw the genus *Astragalus* on the screen telling us that he has found it necessary to recognize eighteen genera in the U. S. instead of one. According to him, two of them even show characters that make it questionable if they are to remain in the same tribe with the others. The pea family is a very difficult one and who can have any objections to changes where they are necessary? But *Astragalus* is not exclusively or even mainly a North American genus. Is it likely that the eighteen U. S. genera will be left untouched and natural after the 1,000 non-American species have been taken into due consideration? I want to say that the making of American genera without due regard for the species in other countries is a dangerous thing, even unscientific in some instances. I shall have the pleasure of referring to a few examples.

In American floras we find the following key to the genus *Vaccinium:*

Filaments glabrous; anthers 2-awned on back; leaves deciduous . . . . .Vaccinium
Filaments pubescent; anthers awnless.
    Ovary incompletely 10-celled, leaves deciduous . . . . .Cyanococcus
    Ovary 4-5-celled; leaves persistent . . . . .Vitis-Idaea

There are, in the Hawaiian Islands, half a dozen species, all being very close together. The filaments are glabrous or pubescent, the anthers always 2-awned, the leaves persistent. Shall we make another or perhaps two new bad genera to

hold these species? Or is it not far better to go back to *Vaccinium* in the older and wider sense? *Oxalis* offers another example. Combinations of a morphological character relating to the subterranean organs and the color of the flower have been used for the segregation of North American genera. They look well enough as long as we restrict ourselves to the species of *Oxalis* in the U. S. But among the numerous Chilean and Andine species we find other combinations of such characters, so there is a need for more equally weak genera. Anybody who is familiar with one of our common species of *Oxalis*, say *O. acetosella,* will automatically recognize the genus from the flower, or even from the leaf, and will call a strange Andean species *Oxalis*, let it have a bulb, or a scaly rhizome, or a leafy stem, and that is, I believe, a good proof of the natural delimitation of the old genus and of its genetic homogeneity.

The other day another somewhat different example happened to come before me. In an American flora I found that *Ranunculus lapponicus* is referred to a special genus *Coptidium* of Beurlin because it is said to be scapose and has the upper portion of the achene empty, flattened and a little spongy. Its nearest relative in our Swedish flora is *R. hyperboreus,* which has the same sort of a trailing stem and auxiliary flowers, but the latter is considered to be a true *Ranunculus* because the achenes are not flattened. Now, what shall we do with some of the species in New Zealand or the endemic things in Masafuera with their basal rosettes of leaves, leafy stem and flattened achenes with an empty upper part?

Indeed, I do not say that either Linnaeus or Bentham-Hooker or Engler-Prantl should rule our minds only because they have been extensively followed by hundreds and thousands of taxonomists, nor that monographers are sacred and must not be attacked. But, on the other hand, is it not remarkable that men like Engler, who worked during a lifetime on *Saxifraga,* or Janczewski, or Focke, who did the same in *Ribes* and *Rubus,* respectively, never admitted more than *one* genus while anybody who works with only the American species feels entitled to split those genera up into half a dozen each. And how can we explain that we find the American Gentianæ divided up between four genera while people who are working with the genus over in China use the name *Gentiana* in a much wider sense? May I suggest that they know more about *Gentiana* as a whole because China is, as it were, the birthplace of the genus, where there are numerous sections overlapping each other and unfit for the splitting process?

What do we gain by splitting? In some cases, in many perhaps, the operation is necessary. If we find a black sheep hidden in an otherwise natural genus, small or large, drive it out, of course, and make a new genus for it, if this be necessary. Nobody will fail to give you credit for that. What if Linnaeus or De Candolle or Hooker did not do so? Never mind them, your investigation has proved that those species had remained in a wrong place because we did not know enough about them. But apart from such instances, what can the reason be for these almost convulsive efforts to segregate everywhere? Some people say there is a good deal of personal vanity at the bottom of it, but that I refuse to believe. A serious taxonomist will do no such thing. No, as Dr. Rydberg told us in his

paper: when a genus becomes "too large" it is time to split it up so that we may get a better oversight over it. I cannot see the point there. As if a large genus would become easier to handle only because we call its sections genera? Have we really got a better and clearer idea of the genus *Cereus* after Britton and Rose cut it up into 75 pieces? Those who think so, deceive themselves. We get lots of new names to remember and scores of new synonyms to keep a record of, that is about all—we do not gain a single thing by making genera sub-tribes and sections genera, but we lose a great deal. We lose the firm hold on good natural groups, we lose useful and pleasing associations of minds, more so if we put, as is done so often now, equal weight on vegetative as on floral characters. We efface interesting facts regarding geographical distribution. I think it is quite fascinating to observe how a genus like *Viola*, a very natural genus indeed, has developed, under different conditions, the dwarf arboreous species in Hawaii, the marvelous rosulate cushions of the high Andes, the tiny scapose annuals of the Chilean semi-desert, the perennials of our temperate hardwood forests and other types. Split up this genus, and that wonderful display of life-forms passes out of sight. Had the Hawaiian species grown in Oregon and the Andean in the Rocky Mountains they would not have been violets any more. For if the genus *Pinus* is split, anything may happen.

Suppose we have a natural genus (taken in a wide, conservative sense) that has developed one section in Europe, another in Asia, a third in America, showing characters that give us certain hints as to the earlier history of the genus and at the same time so well separated from each other that the splitter has a fair chance to set to work, will it not appear to us that we know, as it were, less about the three new genera than about the single old one unless we are able always to remember that, once upon a time, the three used to be one?

Certainly it is impossible to make, and more so to enforce, universal rules as to what shall be recognized as a genus, and what not. Characters of supreme importance in one family are of small account in another. The limitation of genera is a matter of both good knowledge—and of the whole assemblage, not only of the species in one section of the area—and good taste.

There is another side of the matter worth looking at. Dr. Rydberg, in his paper referred to above, says that as we need small species we also need small genera. But as far as I can understand, these things have nothing to do with each other. We may very well favor small species and still want to retain the genera in a wider sense, for those units are certainly based on somewhat different principles.

Much more could be said, and the examples could be multiplied, but I want to be as brief as possible. It would be well if those who are less keen on changes for changes own sake would join in an appeal to those who believe that change in taxonomy always means development, asking them, before they spoil a good old genus, to stop and ask themselves: what does botany gain? Are not, after all, these new genera like rockets, rising with brilliancy only to slump down and fall into oblivion, increasing the burden of synonyms that all of us curse?

ROUND-TABLE DISCUSSION: BOTANICAL NOMENCLATURE[1]

Note of the Secretary for Taxonomy: This discussion was held under the auspices of Section L (Taxonomy). Formal papers were read by Dr. John Briquet, Dr. Marshall A. Howe, and Professor M. L. Fernald. A paper by Dr. N. L. Britton was read by Dr. Marshall A. Howe.

JOHN BRIQUET

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The Nomenclature Section of the Third International Botanical Congress, held at Brussels in 1910, carried towards completion the work of the Vienna Congress (1905) on the international rules governing questions of nomenclature. The combined result of the decisions reached at Vienna and Brussels has been published in the second edition of the "International Rules of Botanical Nomenclature."[2]

There remained, however, certain points which had to be settled by the Nomenclature Section of the next botanical congress. This congress was to be held at London 1915, but the outbreak of the war in 1914 prevented it.

The program of work for the next congress was defined by the Congress of 1910 as follows.[3]

1. To fix the starting-point for the nomenclature[4] of
   a) Schizomycetes (Bacteria)
   b) Schizophyceae (excepting Nostocaceae)
   c) Flagellatae
   d) Bacillariaceae (Diatomaceae)

2. To compile lists of *nomina generica utique conservanda*[5] for
   a) Schizomycetes
   b) Algae (incl. Schizophyceae, Flagellatae etc.); new lists for groups not included in the list of 1910 and also a supplementary list;
   c) Fungi
   d) Lichens
   e) Bryophyta

3. Compilation of a double list of *nomina generica utique conservanda* for the use of palaeobotanists.[6]

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[1] Arranged by the Section for Taxonomy, of the International Congress of Plant Sciences, Ithaca, New York, Aug. 19 and 20, 1926.

[2] Règles internationales de la Nomenclature botanique adoptiés par le Congrès international de Botanique de Bruxelles Vienne 1905. Dieuxième edition mise au point d'apres les decisions du Congrès international de Botanique de Bruxelles, 1910, publiae au nom de la Commission de rédaction du Congrès par John Briquet, rapporteur genéral. Jena, 1912. G. Fischer, editeur.

[3] Actes du III Congrès international de Botanique 1: p. 85. Bruxelles, 1910.

[4] Règles internationales de la Nomenclature Botanique, éd. 2. p. 14, Art. 19.

[5] Règles internationales de la Nomenclature Botanique, éd. 2, p. 74.

[6] Règles, éd. 2. p. 15, art. 20.

4. Discussion of motions relating to new points which were not settled by the rules adopted at Vienna in 1905 and at Brussels in 1910.[7]

The carrying out of this work was entrusted for points 1, 2, and 3 to two committees under the direction of a rapporteur général, Dr. John Briquet (Geneva, Switzerland), assisted by a vice-rapporteur, Prof. Dr. H. Harms (Berlin). In the compilation of the lists of *nomina conservanda,* the rapporteur général expected the assistance of a certain number of editors in each committee. The committee for cryptogamic nomenclature consisted of 53 members; editors: Prof. V. Schiffner (Hepatics), J. Cardot (Mosses), Prof. Maire (Fungi), Prof. G. Senn (Flagellatae), Prof. N. Wille (Schizophyceae), Dr. A. D. Cotton (other Algae), Dr. A. Zahlbruckner (Lichens). The paleobotanical committee was finally composed of 14 members with Prof. Harms and Dr. Halle as editors.

The editorial committee (Commission de Rédaction) was composed of: Dr. John Briquet, rapporteur général; Prof. Dr. H. Harms, vice-rapporteur; Prof. L. Mangin, Dr. A. B. Rendle. The rapporteur général and the vice-rapporteur were also members of the cryptogamic and paleobotanical committees. The Brussels Congress decided that the editorial committee should function as a Permanent Bureau of Nomenclature till the next congress, where the nomenclature question was to be taken up again. This was certainly a very wise decision, assuring continuity in work which is an absolute necessity.

How and how far has the work been carried out?

The first task of the Editorial Committee was the "mise au point" of the "Rules of Nomenclature" according to the decisions of the Brussels Congress and the publication of the "Rules." This task was achieved with the publication of the second edition of the "Rules" in 1912. I wish to express here again my very warm thanks to my friends and collaborators Harms, Rendle, and Mangin. Harms translated the "Rules" into German and Rendle into English. Both, and also Mangin, made important corrections and additions and also useful suggestions regarding my manuscript. I have also to thank the publisher, G. Fischer at Jena, who accepted the task of printing and publishing the second edition entirely at his own risk.

As soon as the Executive Committee of the London Congress was constituted and had sent its first circular (October 1, 1913), the rapporteur général sent his two first circulars. The first one (November 20, 1913) was addressed to the members of the paleobotanical committee giving new names of paleobotanists in addition to those elected at Brussels, in conformity with a decision of the third congress that the committees could be completed by coöptation.[8] In this first circular, Professor Harms was proposed as editor for the list of validly published and generally admitted generic names of recent plants when they come in conflict with older paleobotanical generic names. Dr. Halle (Stockholm) was proposed as editor for the list of validly published and generally admitted generic

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[7] Actes, p. 86.
[8] Actes, 1. p. 76.

names of fossil plants, when they come in conflict with older homonyms of recent plants which have become synonyms, in order to avoid their being further utilized. Harms and Halle accepted these functions and their election was confirmed unanimously by the paleobotanical committee. The work of the two editors has been interrupted only by the war, in 1914.

The second circular of the rapporteur général was issued on December 20, 1913, and sent to all members of the Committee for Cryptogamic Nomenclature. It gave the exact composition of the committee and indications about the mode of redaction of the lists of *nomina generica conservanda*. The work had been carried out very far when it was interrupted in August, 1914, by the war. The rapporteur général has in hand the lists elaborated by Prof. Vuillemin for Schizomycetes and Microsiphoneae, with proposals relating to the starting-point of nomenclature for Schizomycetes, Myxobacteriaceae, and Microsiphoneae. H. Peragallo sent a list of *nomina conservanda* for Bacillariaceae (Diatomaceae), with proposals for the starting-point of their nomenclature. From A. D. Cotton, I received a supplementary list of *nomina generica utique conservanda* for Algae. G. Senn sent a list of *nomina generica conservanda* for Flagellatae with a proposal of the starting-point of generic nomenclature in that group. R. Maire elaborated a similar list for Fungi.

It results from the preceding indications that the work was very well advanced in August, 1914, and that the greater part of the manuscripts was ready at that time. The documentation thus brought together will have to be submitted to the cryptogamic committee and handed over to the nomenclature section of the next botanical congress.

The second circular of the Executive Committee of the Fourth International Botanical Congress to be held at London 1915, issued January 15, 1914, was entirely relating to the completion of the "International Rules for Botanical Nomenclature," and to the program of work for the palaeobotanical and cryptogamic committees. This circular repeated mainly the contents of circulars 1 and 2 of the rapporteur général. It gave detailed information about the functions and program of the committees, the form in which motions must be drafted and presented, the mode of communication of the motions to members of the Committees; the editing, printing, and sending of a supplement to the "Rules" by the rapporteur général; the time within which all this was to be done, etc.

Important in this second circular is the following item 1, which is strictly comformable to the decisions made at Brussels in 1910.

"The Rules of Nomenclature adopted at Vienna in 1905 and at Brussels in 1910 remain in force. Additions may be made to the present code only: (1) in the form of rules bearing on new points not covered by the decisions of 1905 and 1910; (2) in the compilation of supplementary lists of *nomina generica utique conservanda,* and in fixing the starting-point for the nomenclature of special groups, as stated above."

The decision of the third congress, summarized in the above item, has been directly inspired by the fear of seeing each congress undo what the preceding had

done and to transform the question of botanical nomenclature into a kind of vestel of the Danaides, an endless work, constantly to be undertaken again. This results also from item 10 of the circular which renders exactly the ruling opinion at that time.

"The revision of the Rules of Nomenclature has already occupied three congresses, namely at Paris, Vienna, and Brussels, and by 1915 the rapporteur général will have followed their details for fifteen years. It is highly desirable from all points of view that this work should be completed in London in 1915, and should cease to occupy the international botanical congresses. We therefore urgently beg botanists in general, and cryptogamists and paleobotanists in particular, to examine carefully these points which still require consideration, and to formulate their propositions in such a manner that nothing may be left over for 1920."

Now in the same year, 1910, in which the Third International Botanical Congress was held, an International Congress of Horticulture was also held at Brussels. There, a sub-section for nomenclature adopted a set of rules relating to the nomenclature of horticultural forms, more especially those of a hybrid nature.[9] These rules were partly in discordance with the rules adopted previously by botanists. The suggested alterations in, and additions to, the International Rules of Botanical Nomenclature to fit them to include garden varieties and hybrids have been summarized and printed by the subcommittee appointed by the Council of the Royal Horticultural Society of London, and sent to the rapporteur général. The well known orchidologist, R. A. Rolfe, has also sent a series of proposals relating to the nomenclature of hybrids, partly in discordance with the international rules, but in general agreement with the decisions of the Horticultural Congress of Brussels. Some other detailed proposals of changes have been formulated which may remain unmentioned here, but I must make an exception for Dr. Rehder, who sent a number of useful suggestions, giving more precision to several articles of the "Rules."

On the other hand, the so-called "American Code" which had not been accepted at Vienna, has continued to find in the United States a good number of zealous and able defenders. Though certainly the great majority of taxonomists all over the world apply the International Rules, the hope that there might be unanimity in doing so has thus not been realized. At the Imperial Botanical Conference held by British botanists at London in 1924, a series of resolutions was adopted, which almost all come back upon questions which had been formerly discussed at length before and at the Vienna Congress, and which stand in contradiction with the International Rules. In his recent very interesting paper "A basis for agreement on nomenclature at the Ithaca Congress," Mr. A. S. Hitchcock seems to admit that a kind of compromise could be effected between the supporters of the American Code and the adherents to the British Proposals, and that the result of this compromise might be incorporated into the International Rules of Nomenclature at the next botanical congress. But it must not be forgotten that only British botanists were assembled at the Imperial Botanical Conference and

[9] Published in Bulletin de la Société royale de Botanique de Belgique **47**: 419-424. 1911.

that taxonomists of other countries have had no opportunity to take part in the discussion. Several of the most important articles in which supporters of the American Code agree with the British Proposals have been seriously criticized by M. L. Fernald and C. A. Weatherby on this side of the Atlantic, and by Schinz and Thellung in Europe, and it is probable that a compromise of that kind will encounter a very strong opposition both in America and in Europe.

Some botanists have expressed to me their astonishment that the rapporteur général has participated in no manner in these discussions. I have not taken part for reasons of principle. A *rapporteur* must remain, as long as he is in function, entirely neutral. He is morally bound to apply as strictly and conscienciously as possible the International Rules in his own taxonomic work, but it is better for him not to take an active part in the discussions preliminary to a congress which has *legislative* aims. When the matter is entirely prepared for discussion, when a competent committee has given its opinion upon the proposals, when he brings the whole business before the Congress, at that moment he may give his opinion, which will then be the more readily taken into consideration, especially in important or difficult cases.

The conclusion of the very rapid preceding review is this: The Brussels Congress has eliminated from the program of the next international congress all motions which do not relate to *new* questions. But the next congress was to be held at London in 1915. Eleven years have elapsed since that time, and sixteen years since the meeting at Brussels. One may say that *circumstances* are *new*. The desired unanimity of taxonomists in matter of Rules of Nomenclature has not been obtained. There are still strong dissidences. We have even seen rules contrary to the international rules adopted by a horticultural congress. Under these conditions, if there is a probable chance, or only a possible chance, of bringing union in 1930, I think that this chance must be taken and that we must try to clear up the situation. The wish expressed by the executive committee of the congress planned for 1915, and by myself, to see the nomenclature question disappear for a time from the program of botanical congresses may perhaps be realized if we try to come to a suitable agreement at London in 1930. Rules of nomenclature, as all other human dispositions, cannot be considered as eternal, but they ought not to be modified unless absolute necessity commands it. A general agreement in 1930 would probably have the consequences of beginning a period of tranquility, leaving more time to essentially scientific work.

I would accordingly make the following proposals:

1. The actual round-table discussion aims at putting in evidence the points of botanical nomenclature which, although they are not new, are still a matter of profound disagreement among taxonomists and upon which it is desirable to secure a general agreement at the Fifth Botanical Congress in 1930.

2. If such an agreement, partial or entire, could be effectively realized now among botanists present at Ithaca, it ought to be presented later on in printed form and in the conditions which the Executive Committee of the Fifth Interna-

tional Congress will adopt for all motions relating to botanical nomenclature in general.

3. Elections at Ithaca of a Committee to which the Rapporteur général could submit all motions presented on these topics, as was the case for Vienna in 1905 and for Brussels in 1910. This committee is distinct from the cryptogamic and from the palaeobotanical committees already functioning. The members of the Permanent Bureau of Nomenclature are members of this committee.

In respect to the third proposal, I must give a short justification. The creation of this committee is a necessity, for the cryptogamic and palaeobotanical committees have special tasks and are incompetent, in their actual composition, for questions of general interest. The committee will not constitute in itself something entirely new, but may be considered as an extension of the Permanent Bureau imposed by new circumstances. It is more in conformity with the tradition of former botanical congresses to create this organization here in Ithaca than to entrust the Permanent Bureau with its constitution.

I close my statement with these proposals, thanking the Organizing Committee of the Fourth International Botanical Congress for having given us the opportunity of this round-table discussion at Ithaca, thanking our friend Hitchcock for having taken charge of it, and expressing the wish that our meeting may have a happy influence upon the success of the Fifth International Botanical Congress.

MARSHALL A. HOWE

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As has already been pointed out by Professor Hitchcock, Mr. Kenneth K. Mackenzie, and others, a very large part of our differences in nomenclature is due to varying conceptions as to the limits of genera—and this is largely a subjective mental matter concerning which no International Congress can ever hope to legislate successfully. To cite only one example of diversity of usage from this source alone, we may remark that thirty-two years ago, Dr. K. Schumann in "Engler and Prantl, Die natürlichen Pflanzenfamilien," recognized 21 genera in the cactus family. In the sumptuous 4-volume monograph of the Cactaceae written by Drs. N. L. Britton and J. N. Rose and recently published by the Carnegie Institution of Washington, 124 genera are recognized—nearly six times as many as were considered valid by Schumann a third of a century earlier. Whatever its merits or demerits, many—probably most—botanists will accept the handsome work of Britton and Rose and its 124 genera as the last word on the subject. And, whatever its merits or demerits, some of the more conservative botanists will doubtless continue to swear by the work of Schumann and its 21 genera, or, perhaps, by Vaupel's revision of the Cactaceae for the second edition of the Engler and Prantl work, with its 26 genera. And there is nothing that we or any rules of nomenclature can do about it!

In the matter of the proposed nomenclatural compromise or agreement, I may say that personally I do not feel so irreconcilable as I may have felt in my younger

days, when I had had less experience with the practical difficulties involved.   The main concession now asked of the supporters of the American Type-basis Code is apparently the admission of long lists of generic *nomina conservanda.* The so-called International Rules, as has been noted by several of its critics, start out with the assertion that "The rules of nomenclature should neither be arbitrary nor imposed by authority" and then close by arbitrarily setting aside several hundred generic names as beyond the reach of law.   Personally, I should have little objection to generic *nomina conservanda* if they were anchored to one of the original species as the type and if the list were limited to the very few cases in which serious confusion might result from a rigid application of the law—such, for example, as the substitution of the name *Marsilia* for *Salvinia,* which would result from a relentless enforcement of the American rules for typifying genera.   But the Brussels Botanical Congress of 1910 added 53 names of phanerogamic genera to the 404 already set aside as above the law by the Vienna Congress of 1905.   The Brussels Congress also listed 55 generic names of algae as beyond the realm of law and indicated that others were to be added at the next congress.   The Brussels Congress also indicated that lists of generic *nomina conservanda* for the bacteria, fungi, lichens, and bryophyta would be presented at a future congress.

This whole matter of the nomenclature of the lower plants has apparently received no attention from the leaders in the proposed compromise, although more than two-fifths of all the described species of plants belong to groups lower than the Pteridophyta.   The Brussels Congress, as is well known, adopted eight different starting-points for the nomenclature of the lower plants and, on the principle that "silence gives consent," the suggested compromise agreement implies the acceptance of this confusing welter of initial points.   The Brussels Congress of 1910 acted on the advice of one or more specialists in each of the principal groups and the results show astonishing diversities, according to the experience, personal preferences, and prejudices of the specialist whose advice was accepted.   For the Myxomycetes they adopted 1753 as the starting-point, with no *nomina conservanda,* —1753, because Miss Lister had adopted that date as a starting-point in the second edition of the Lister monograph of the Mycetoza, then in press,—1753, although Linnaeus knew little or nothing of the Mycetozoa and no one of the generic names used by Lister is attributed to Linnaeus.

For the algae, the Brussels Congress adopted 5 starting-points and a list of 55 generic *nomina conservanda* besides.   The general starting-point for the algae, according to that Congress, is Linné's Species Plantarum, 1753, but for the Desmidiaceae, 1848, the date of Ralf's book on the British desmids, was taken; for the Nostocaceae Heterocysteae, a group of "blue-greens," 1886, the date of Bornet and Flahault's monograph of the representatives of the group contained in the principal herbaria of France; for the Nostocaceae Homocysteae, 1892-93, the date of Gomont's monograph of the group, likewise based on specimens found in French herbaria; and for the Oedogoniaceae, 1900, the date of Hirn's monograph of the family.

For the fungi, 2 starting-points were adopted.   For the rusts, smuts, and puff-

balls, 1801, the date of Persoon's "Synopsis"; for the remainder of the fungi, a sliding date, 1821-32, the date or dates of Fries' "Systema Mycologicum."

For the Muscineae, with the exception of *Sphagnum,* 1801, the date of publication of Hedwig's "Species Muscorum," with a list of *nomina conservanda* to follow; for *Sphagnum,* 1753. For the Hepaticae and Lichenes, 1753, with lists of *nomina conservanda* to be arranged later.

For the Pteridophyta, the starting-point is 1753, with only one *nomen conservandum—Selaginella.* Now it had happened that, following the Vienna Congress of 1905, Dr. Carl Christensen of Copenhagen busied himself with compiling and publishing his "Index Filicum," with priority principles applied and that the Brussels Congress in 1910 found the idea of starting the nomenclature of the ferns with 1753 rather commonly accepted. Hence 1753 as the starting-point of the nomenclature of the Pteridophyta, with only one generic *nomen conservandum—* just as they voted 1753 as the starting-point for the nomenclature of the Myxomycetes with no *nomina conservanda.* If we had only had some one to do for algae and fungi, previously to 1910, what Lister did for the Myxomycetes and what Christensen did for the Pteridophyta, if we had had some one to show us that the results of applying priority principles to the algae and fungi, with 1753 as a starting-point, are not so horrendous as some people seem to suppose, the nomenclature of those two great groups might perhaps now be in as satisfactory and stable a condition as is that of the Myxomycetes and Pteridophyta. To ask us now to approve, even by implication and silence, the numerous and incongruous starting-points of the so-called International Rules, is, in my opinion, to ask us to take a confused and backward step. Why should any student of the Oedogoniaceae, for example, pledge himself not to go back of Hirn's excellent monograph, published in the year 1900? Hirn was a young and doubtless fallible human—28 years old on that date. The monograph was, I believe, his doctorate thesis. Why, by a vote of an International Botanical Congress, try to make this thesis inerrant scripture for the naming of a small group of plants—a group of no economic interest and virtually unknown except to the specialist? Is it quite honest and reasonable to do this? Is it good science? Various ecclesiastic councils in times past have by majority votes taken somewhat similar action in regard to documents more or less hallowed by age and by outstanding merit, but such action has met with only temporary and local success. If we must really have more than one starting point for the nomenclature of plants, why should we be content with only eight? There are other most excellent generic and family monographs besides Hirn's monograph of the Oedogoniaceae with its two genera!

If we must have lists of generic *nomina conservanda,* let the lists be very brief, comparable to *Selaginella* for the Pteridophytes. And let us not now approve, even by implication, a confusing and time-serving multiplicity of starting-points for botanical nomenclature!

The International Rules of Zoological Nomenclature recognize only one starting-point, 1758, for all groups of animals, and they recognize no *nomina conservanda* as such. However, the rules, under specified conditions, confer plenary power

upon an International Commission on Zoological Nomenclature to suspend the rules "as applied to any given case, where in its judgment the strict application of the Rules will clearly result in greater confusion than uniformity." Possibly the establishment of an International Commission or a Supreme Court of nomenclatural experts, to which doubtful questions could be referred, would be a distinct aid in the attempt to standardize botanical nomenclature.

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Professor Hitchcock's invitation to me to take part in this discussion read: "I am writing to ask if you would be willing to represent the advocates of the International Rules at this discussion?"[1] The implication seems to be that at this international congress the International Rules need a special advocate or defender; and since, with my colleague, Mr. Charles A. Weatherby, I have very recently expressed[2] my reactions to some of the changes proposed, I can do no better than to reëmphasize certain of these points. It may be of interest, in view of our general desire for agreement, to call attention at the start to one of the responses stimulated by Mr. Weatherby's and my issuance of our views. One American botanist, for instance, referring to our plea for the retention of Latin diagnosis, wrote: "I like the Latin names and think all well-trained scientists do. Count me on the side of conservatives in general. . . . . I strongly approve of Dr. Hitchcock's and your views." It should be clear, then, that, although called upon "to represent the advocates of the International Rules," I am sometimes considered by my colleagues as in full agreement with Professor Hitchcock.

I may now be pardoned if I read what are familiar to some of you, portions of the circular letter in which Mr. Weatherby and I have already expressed our views of certain of the proposed changes.

Professor A. S. Hitchcock has for several years been active in trying to induce followers of the International Rules of Nomenclature to "compromise"[3] with the American botanists who have refused to follow the majority rulings of the international congresses of 1905 and 1910. In this effort he has cooperated with the Brittish Imperial Botanical Conference and it is now proposed that American followers of the International Rules shall indorse the proposals made for the al-

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[1] Hitchcock in letter of May 29, 1926.

[2] Fernald and Weatherby, Comments on the Proposals of the British Imperial Botanical Conference for modification of the International Rules of Nomenclature. Circular Letter, issued December, 8, 1924.

[3] In the discussion which followed the formal presentation of papers, Mr. Sprague stated that the word "compromise" had had no place in the propositions of the British Imperial Botanical Conference. In the statements of the British propositions issued in America by Professor Hitchcock, including his paper, *A Basis for Agreement on Nomenclature at the Ithaca Congress*, Am. Journ. Bot. xiii. 291-300, issued in May, 1926, and distributed shortly before the Ithaca meeting, the word is very definitely used: "Other resolutions adopted [by the Imperial Botanical Conference] were the following which bear especially upon a compromise between the two codes."

teration of the International Rules. Since many of these propositions are reversals of the decisions of the international congresses of 1905 and 1910 and are merely the old points of difference presented anew, it is important that they be fully understood. Professor Hitchcock has been active in making known his views; the subject has been closely studied and ably discussed in England, chiefly by Mr. Sprague; Mr. K. K. Mackenzie has issued a circular letter upon the subject; and, after solicitation by several botanists, we have decided to issue the following comments upon some of the British proposals which have been transmitted by Professor Hitchcock.

1. Abolishing the requirement of Latin diagnoses in the publication of new groups.

Latin is necessarily known to all taxonomists. No real progress is possible in taxonomy without ability to consult the fundamental works and the great monographs, chiefly in Latin. With this necessary modicum of knowledge and the older models to follow it is not difficult to construct a diagnosis which, though perhaps lacking in elegance and classical finish, is readily intelligible to systematists everywhere. This concession to international intelligibilty and convenience is far simpler than the alternative of being forced to decipher diagnosis in many tongues, which would inevitably soon include those of non-Latin origin. The value and general intelligibility of Latin are so apparent that even some followers of the American Code use it when they wish to reach a wide audience.

The Latin diagnosis is a practical international convenience. On this account and as a defense against diagnosis in tongues quite unfamiliar to the majority of botanists, it should be continued.

2. Rejecting all combinations which are homonyms.

The principle of the International Rule, that no combination in itself invalid should prevent the validity of a later use of the same combination, is sound. In practice, however, it is often difficult to determine whether a given name is universally regarded as a synonym, and in all cases of doubt we favor rejection of the later homonym.

Certain names are invalid beyond doubt and their existence should not invalidate the later valid use of the same combination for a different plant. Such are: (1) *Nomina nuda;* (2) direct and conscious renamings of species already validly named, such as were freely indulged in by Salisbury, Sprengel and Rafinesque; (3) names of species demonstrably based on the same types as species already validly named.

The provision of the International Rules, as amended at Brussels, that a name invalidated by an earlier homonym may be validated by transfer to a new position, if the author who first makes the transfer so chooses, works well in retaining familiar names and thus avoiding the needless coining of new ones. E. g. *Aspidium nevadense* D. C. Eaton (1878) is antedated by *A. nevadense* Boiss. (1838). Baker, in first transferring the species from *Aspidium* to *Nephrodium* (1891) rightly, as it seems to us, validated Eaton's name, as did Underwood (1893) in placing it under *Dryopteris* as *D. nevadensis.* Christensen, however, following the method

of the American Code, made a new and needless name for the species under *Dryopteris, D. oregana* (1905). By the International Rules, Underwood's combination would stand under *Dryopteris,* and no new name would be necessary. The desirability of retaining the provision will be apparent to those who are striving to avoid unnecessary changes.

Another group of names which it would be unfortunate to displace are well established and clearly defined botanical names which may be invalidated by earlier homonyms inadequately or vaguely published *(nomina subnuda)* or names which have received only horticultural definition.

If the overthrow of later but otherwise valid homonyms by early invalid or inadequately published homonyms can be avoided we feel confident that no serious opposition by followers of the International Rules to the adoption of this proposal will be made.

3. Rejection of generic homonyms, except such as may be specially conserved.

The same principle as just discussed plus the use of *nomina conservanda* as proposed, should apply to generic homonyms: no indubitably invalid names should prevent the later valid use of the same name.

4. Formally accepting the principle of the "Type-method" of applying names.

The principle of types is already accepted and has long been so, at least in some form and degree, by everybody; the point in dispute is the method of applying it. We cannot see that the proposed rules for choosing the types of genera are likely to bring any greater stability and uniformity of usage than at present exist. There is inherent difficulty (to say nothing of futility) in forcing upon the work of old authors a conception of types which never entered their heads. The number of alternatives it has been thought necessary to provide proves this, if proof were needed. Their very number offers large opportunity for such differences of opinion as that which has arisen between Drs. Britton and Maxon in regard to the type of *Pteris* (Jour. Bot. 61: 7); in fact it makes them almost inevitable. There is no possible guarantee that others will show so much respect for current usage and proceed in so conservative a manner as Prof. Hitchcock is disposed to do.

The "type-basis rules" are so nearly those of the American Code that their workings may fairly be inferred from the operation of the latter. Under it a number of the most confusing and deplorable sort of changes have occurred, the shifting of universally familiar names to unfamiliar applications. *Sisymbrium, Erysimum* and *Leontodon* of the 2d edition of Britton and Brown's Illustrated Flora and of the Flora of the District of Columbia are cases in point.

In very many cases, the application of old names has already been definitely fixed by unanimous or practically unanimous current usage (excluding recent changes due to the application of the American Code). There we have only to let well enough alone. The principle of the *nomen conservandum* should be applied, as has been suggested, not only to the names themselves, but to their application. The reasons for conservation have equal force in either direction. Where there is diversity in usage, the doctrine of residues offers the simplest and

most definite means of fixing the application of names. It is surely more logical to work forward from large and involved to smaller and definite groups, following the conceptions of the authors who simplified the complexity, than to work backward from a retroactively chosen type. Once the group to which a given name should be applied is determined, the type species will often choose itself. Of *Erysimum*, for instance, in the generally accepted sense, *E. cheiranthoides* would automatically become the type, being the only one of the original species left after the other generic entities had been withdrawn from the original complex *Erysimum* of Linnaeus.

5. Acceptance of "duplicating binomials," such as *Linaria Linaria*.

Compared with the other changes proposed, this is relatively unimportant. Duplicating binomials have been rejected by the greatest systematists and authors of large Floras of the past, Bentham, Blytt, Boissier, Robert Brown, the De-Candolles, Fries, Gray, Greene, Hartman, the Hookers, Koch, Lamarck, Lange, Ledebour, Nees, Rouy, Torrey and practically all the others; and the long-established botanical usage should not be altered without necessity. The instability complained of by Mr. Sprague as due to the rejection of tautonyms is no greater than that which attends the search for the earliest available name where tautonyms are not concerned.

6. Rejecting the "principle of nomina abortiva."

Discussed by us under nos. 2 and 3.

7. Revision of the list of *nomina conservanda*.

Certainly errors or doubtful cases should be eliminated or defined. But a revision on the lines suggested by Mr. Sprague's remark that the list contains names which, *though current,* are not important enough to be conserved, might well defeat the purpose of the list, which is, of course, to preserve *current* usage. We should not approve a revision primarily intended to cut down the list. Mr. Mackenzie, in his circular letter of November 3, 1924, insists that the recognition of any *nomina conservanda* is dishonest, in that it does not give just consideration to the botanist whose name is excluded. But just consideration to the botanists of the present and future is far more important. The names of plants constitute a language used for intelligible communication among botanists. In this, as in all other languages, usage is a primary factor. We do not insist that injustice is done to the coiners of English words now obsolete because others more generally understood have been conserved. (See General Comments at end of this communication.) Personally we are willing to go even further than the conservation of generic names and to apply the principle to the names of species of first economic importance or to those whose names become completely reversed through the application of an exact method.

8. Making clear how far each of the Nomina conservanda is conserved.

If this means that the application of conserved names should be defined, we heartily agree.

GENERAL COMMENTS

As American botanists who have accepted the International Rules in good faith and have aimed consistently to follow them, we find some of the proposed changes undesirable. It is too often forgotten that nomenclature is not a branch of historical research and not for the use of the professional taxonomists alone, but a practical device, analagous to language. As such, it suffers from every change made for purely nomenclatorial reasons. It is the great merit of the International Rules that they recognize this practical side.

The International Rules were adopted after years of detailed preparation, by a democratic congress of leading systematists representing 17 countries (counting the British Empire as 1). The article about which there has been most discussion (the recognition of *nomina conservanda*) was adopted by a vote of 133 to 36. These figures have been sometimes represented in this country and in England as a result of "manipulation" of the convention by a *"German* majority." But since the maximum Germanic vote (including Austrian and Hungarian) in the convention was 64, it is clear that the majority-total contained at least 69 non-Germanic votes as against the minority vote of 36. Certain American botanists who were in the minority have refused to accept the majority ruling and as a result we have in this country the American Code and its offspring, the Type-basis Code. And the followers of the International Rules are asked to "compromise" with those who have not followed the International Rules on a basis of 5 points for the minority to 3 for the majority in order that we may have an International Code.

The Americans who have accepted the International Rules worked long and ardently for certain practical and time-saving principles, notably for the "Kew Rule" for specific names. This principle, if it had prevailed, would have saved 90 per cent of the changes in specific names which have resulted in America from the adoption of the International Rules. It was lost, but its defenders accepted the majority decision and have felt it a matter of honor loyally to uphold the majority ruling. It is admitted by Professor Hitchcock that followers of the International Rules constitute at least one-half the American botanists; and that those who do not follow them are only a small minority of the botanists of the world. It certainly is not worth while for the majority of botanists to make undesirable changes in nomenclature in order to attract the adhesion to those who, by their past action, have shown unwillingness to accept majority decisions which do not wholly coincide with their wishes. In accepting the International Rules, those who had followed and urged the Kew Rule gave up much more than the followers of the American Code would have had to give up had they also accepted them. *The International Rules are themselves a compromise,* reached by sacrifice on many sides. We may be pardoned if we do not hasten to make further and undesirable compromises for the sake of a uniformity which, after the experiences of 1905, we cannot but fear will prove illusory.

Nevertheless, if the proposals are adopted by a truly representative and duly constituted international congress, we will, of course, accept them, as before.

Would those Americans who are now urging "compromise" be equally ready to accept an adverse decision of such a congress? If so, a real step toward uniformity would be taken.

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"Nothing is constant but change" is a feature of human experience in all lines of activity, often lost sight of, but always with us, and to some people a very troublesome factor in their existence. It is, indeed, in the nature of an inexorable law from which there is no complete escape. Like other natural laws it is probably beneficial in the long run, and may therefore be regarded with more consideration than is often awarded it. We meet it everywhere in the domain of natural science. All attempts to nullify or evade it have only been partially successful, and future trials must have the same fate. Names for objects, places, and organisms come quite within the influence of this law of change; our puny endeavors to stabilize them by rules and legislation can only meet with partial success, and the history of botanical nomenclature is a salient illustration of partial failure, when considered in the operation of its details. Modified conceptions of generic limitations, apparently impossible and probably undesirable to control, put a large percentage of binominals into necessary instability.

As regards the applicability of any elaborate and therefore complicated series of nomenclatorial rules, there will always be some uncertainty in results, and the amount of time and effort required in the attempt to follow them may well be considered, as compared with the conclusions reached by individual students; examples of this are common in literature, differences in interpretation of rules being frequent by the followers of any code.

The advantage of simplicity, with the expectation of some diversity in nomenclature, as against complexity and the futile attempt at absolute uniformity, may, therefore claim consideration at this period of discussion. If approved, it requires allegiance to a few principles only, and, as long ago pointed out, these must neither be arbitrary nor imposed by attempted authority; otherwise they will be resented, and fail in their purpose.

The American Code of Botanical Nomenclature modified in some details by the Type Basis Code, is an attempt at simplification of the International Rules, based on a few principles, and a protest against arbitrary features of those rules. The outlined application of these principles is, perhaps, still too complicated; the emphasis laid upon the basing of species upon type specimens and of genera upon type species, and the complete rejection of hyponyms there first elaborated, are among its most important features and have demonstrated their value, as evidenced by wide acceptance; modification of some details may well be deemed desirable in the light of experience.

But the rejection of generic names properly typified, for the sole reason that their acceptance would change binominals in current usage is arbitrary, autocratic,

and unscientific, therefore abhorrent, repellent, and unwise. The abandonment of the theory of *nomina conservanda,* as at present understood by its misguided advocates, is therefore necessary before a rational system of botanical nomenclature can be obtained. The application of the principle of rejection of hyponyms and of homonyms, should, together with the selection of type species, operate to bury enough debatable generic names to meet all actual requirements, and avoid attempted artificial conservation of names.

Consideration of the international rules of zoological nomenclature will suggest a method for avoiding the use of some generic names without invoking the highly arbitrary one here denounced; these rules have recently been republished by the Biological Society of Washington (Proceedings **39**: 75-104).

SIGNIFICANCE OF TAXONOMIC UNITS AND THEIR NATURAL BASIS[1]

FROM THE POINT OF VIEW OF TAXONOMY

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In the ideal system of classification all units have a natural basis. Whether or not a system so magnificent, one in which each unit appears in its proper phylogenetic setting, can be eventually discovered in all its details, is open to question, but the attainment of a goal so desirable is well worthy of the best efforts of all progressive biologists.

In order that taxonomic units be natural it is essential that their natural boundaries be known. This necessitates a knowledge of relationships, which consideration leads, in turn, to the inevitable conclusion that phylogeny must be the basis of classification. It is true that the founders of the science of taxonomy possessed no concept of phylogeny in the modern sense, and that credit for our present system is due in large part to workers with little or no thought of natural relationships; but since the time of Darwin the most notable advances have been made by some philosophic taxonomists who have kept the picture of evolutionary lines clearly in mind, and all signs point to phylogeny as the guiding principle of the taxonomy of the future.

If, then, phylogeny is to be the basis of classification, much thought should be given to the methods whereby phylogenies are determined. This is only another way of saying that the methods commonly used in evaluating taxonomic criteria should be more carefully scrutinized and new methods developed. It is, however, both unjust and useless to berate taxonomists for their hasty work and sometimes unscientific methods. On the other hand, it is of the highest service to develop and apply new methods in taxonomic research.

In the past, taxonomic criteria have come largely through studies in comparative morphology, with some assistance from paleontology, embryology, and other sciences. Far too often, it must be admitted, personal judgment based upon very slight evidence, has determined the limits of the units. But with the recent rapid rise of cytology, genetics, experimental ecology, and serology, there now becomes available a mass of evidence hitherto undreamed of. That this evidence is not readily accepted by the taxonomist is due in part to a natural disinclination to familiarize oneself with a new field, but also, and in large measure, to the suspicion that it is not so trustworthy as the specialists in these fields would like him to

believe. The systematist is a conservative. He is fearful that workers in these related fields may be self-deceived by their own enthusiasm, and hence he awaits presentation of the final proofs.

That this, however, is a passing phase is evidenced by recent *rapprochements* between taxonomists, on the one hand, and cytologists, geneticists, ecologists, and biochemists on the other. This should result in great benefit to all workers, for all are vitally concerned with the two great central problems, heredity and evolution. The objective of all is to contribute towards a knowledge of these fundamental processes, both as to methods and results.

The latter (results) are of especial interest to the taxonomist. They are the materials with which he works, the genera, the species, and the smaller taxonomic units; but he needs also to know the steps whereby these results were obtained. Only thus can his dream of a complete classification be realized. For taxonomic units are of significance only insofar as they are evolutionary units.

But a detailed knowledge of the methods and results of evolution is equally vital to the other groups of biologists just mentioned. All are concerned and all must contribute towards the final solution of the problem. This central problem of evolution will resolve itself only after there has been effected a combination of all the viewpoints.

The cytologists, geneticists, and ecologists, much too often confined to the laboratory and garden, may work out in great detail the mechanism of heredity or the influence of environment and yet fail to grasp the significance of these features in the broader field of evolution. The significance of the laws of geographic distribution may still be unappreciated. The sympathetic understanding which comes only from much consideration in the field may be lacking. On the other hand, the taxonomist who is limited to field and herbarium studies denies himself that insight into evolutionary processes which can come only through detailed laboratory and garden experiment.

It is for the former groups of investigators (the geneticists and ecologists) to show how nature supplies the materials and the opportunities for organic evolution and to portray the first steps in this process; it is for the taxonomist to demonstrate how the units thus supplied are sorted out and finally built up into the evolutionary tree with its myriads of branches and complicated twiggery.

There have been artificially produced, for example, plant forms that seem as distinct from previously known forms as any generally accepted species is from any other. I refer particularly to the so-called species artificed through hybridization, tested by the laws of genetics, and interpreted in the light of cytology. But nothing is known as to how these forms would react to a natural environment with its competition of similar but natural species, and even though species thus artificially created were to stand the test of natural requirements, it would not demonstrate that all evolution had proceeded by this process.

It therefore remains for the systematist, or phylogenetic taxonomist, with his knowledge of character values, the laws of geographic distribution, and the effect

of isolation, to demonstrate how the smaller units have become organized into the great evolutionary tree. But there still remains the need of the master mind that can visualize the entire process, from the first chemical changes to the final completed structure. Such a mind would need to handle with ease the concepts of physical chemistry and genetics at one extreme, those of taxonomy and geographic distribution at the other.

While awaiting this super-scientist to appear, the only hope for utilizing the results of studies in widely separated fields as a basis for determining the proper sequence and hence the significance of taxonomic units lies in cooperation between the workers themselves.

A sympathetic synthesis of the viewpoints of specialists in different fields would greatly accelerate our advance. It might lead to a comprehensive theory of evolution more closely approximating the truth than any that has gone before. This would necessitate a drawing together of evidence from all possible sources and a complete understanding between workers in the diverse fields of biology.

Reference may here be made to a beginning in this direction. In an attempt to determine the natural basis for the taxonomic units comprised within the collective species, *Hemizonia congesta*, a joint study was made by Professor E. B. Babcock and the writer. This involved genetic, cytologic, ecologic, and taxonomic methods and viewpoints and included intensive studies in geographic distribution. The result is shown in the accompanying chart (Fig. 1). It is seen that it was possible to bring all of the forms into six major groupings. These are designated as subspecies, since they represent the emergency of phyolgenetic lines from the great maze of connecting forms. It may be surmised that, given abundance of time and suitable barriers, each of these might become a species, at once as distinct from its neighbors and as complex within itself as is the collective *Hemizonia congesta* at the present time. Between these subspecies lie hybrids, first recognized in the field from their characters and distribution, later experimentally produced in the cultures. Within each subspecies lie minor variations, many more, in fact, than are indicated on the chart. These occur also between the subspecies. Some of these are genetic units, as determined by cultural tests, others are temporary ecologic responses, as determined by transplant experiments.

The detailed evidence upon which this arrangement rests is presented elsewhere (Univ. Calif. Pub. Botany **13**: 15-100. 1924). This very incomplete and comparatively simple case of cooperative endeavor is here presented merely to indicate something of what might be accomplished in larger fields, and with an enlarged corps of cooperating botanists and chemists. We feel very strongly our handicap in not being able to view such problems from all possible angles.

The present paper, therefore, constitutes a plea for the cooperative testing of the significance of taxonomic units. This can best be brought about through a further extension of the methods of taxonomic research, especially in the direction of exact experimentation, and through the interpretation of all evidence from the combined viewpoints of taxonomy, ecology, genetics, biochemistry, and related subjects.
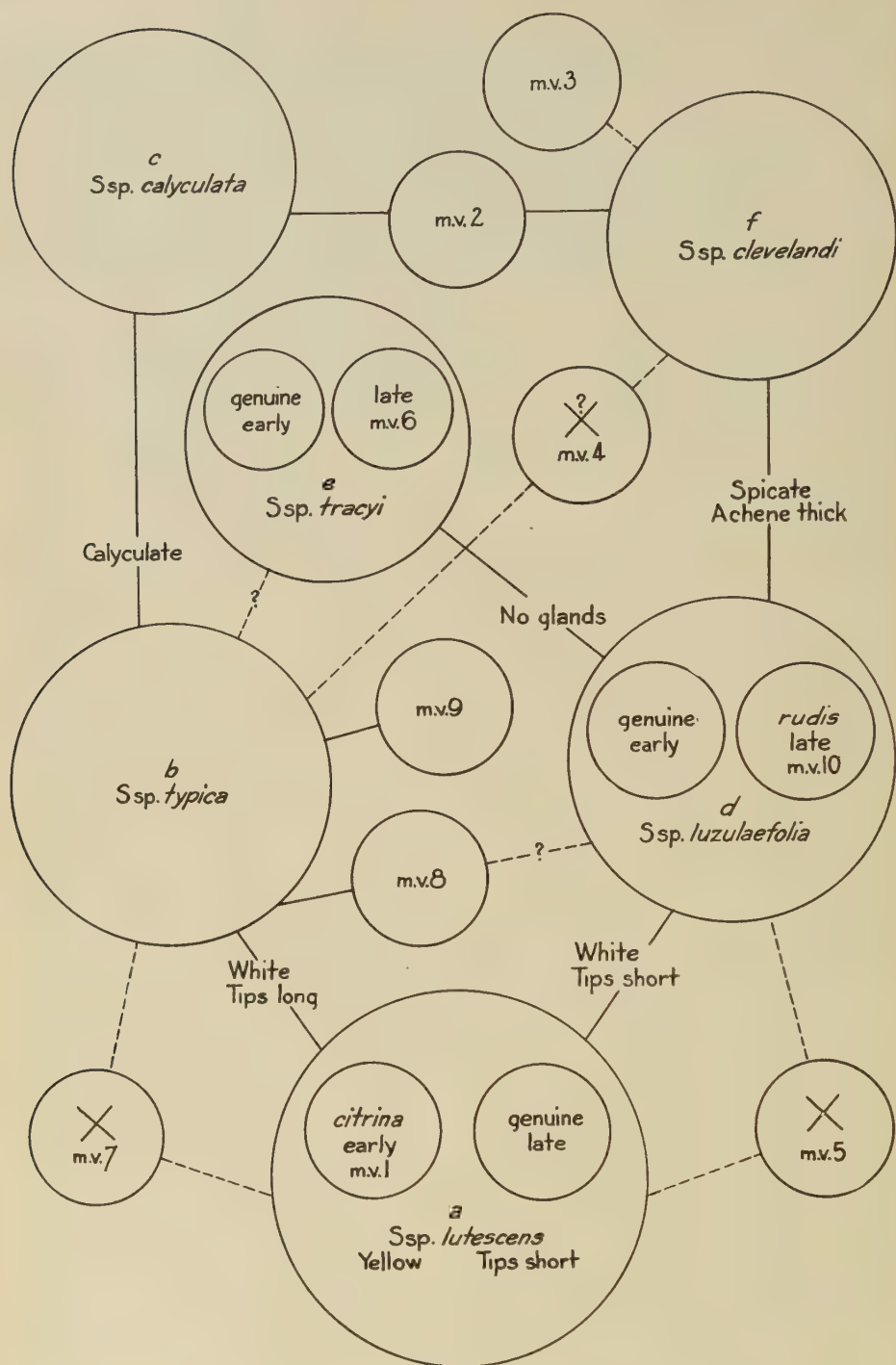
FIG. 1.

DISCUSSION OF DR. H. M. HALL'S PAPER

K. M. WIEGAND

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I was much surprised a few years ago, on the publication of Hall and Clements paper on "The phylogenetic method in taxonomy," to learn that taxonomists in general were not concerned with the interpretation of phylogeny in the groups that they were revising, for I had supposed that the aim of all work in taxonomy since Darwin's time was to detect if possible the "blood relationship" of organisms. Of course most of the older taxonomists did not concern themselves with blood relationship, as they were not evolutionists, but in modern times there would seem little excuse for any other point of view.

With regard to the question of experimental taxonomy from the standpoint of genetics and ecology I fear that I stand with de Wildeman in his paper before the Section for Taxonomy in the belief that while data obtained in this way are very desirable and are often capable of throwing great light on the significance of morphological differences, they are not usually of practical value to the general taxonomist. Such data are often impossible to obtain, sometimes because of the unavailability of the living material, sometimes because, as in the case of woody species, the time required to grow the plants is too great, but often also because of the large number of plants concerned.

A few words may be said regarding the units to be recognized below the genus, and their definitions. I have little sympathy with those who say that species are wholly subjective and arbitrary concepts created for convenience only. I believe that most taxonomists feel that species are real, and actually exist in nature. I think everyone will admit that the concepts of dog, cat, cow, horse, pea, bean, and corn, are real. Yet these are species differing in no fundamental way from others with which the taxonomist has to deal. The taxonomist feels toward his species exactly the same as we do toward the concepts mentioned above. However, the units that exist are by no means all of the same grade, but are in fact very diverse in value. Which units we shall call species, and what the other units shall be called is a question. After many years I have come to believe that the species must be of practical value, especially since it carries with it the name of the plant. Units that can not be recognized or that grade into others are scarcely practical as species. I am inclined to define a species somewhat as follows: A group of individuals that can be recognized with reasonable ease by the average botanist as distinct from other groups of individuals. In this concept the two important features are the distinctness of the group (morphologically in the case of the higher plants) and the reasonable ease of recognition. A subspecies to me would be a group, still distinct but difficult to recognize because of the fineness of the distinctions. A variety would not be distinct but would grade into other varieties, and a form would be of sporadic occurrence. I do not object to the recognition of minor units based on other considerations, such as elementary species, strains, etc. The special student of plants from the standpoint of genetics

must, of course, represent what he finds by a classification suited to the occasion, and it is right that he should. This should not make necessary, however, the abolition of the broader taxonomic species.

I am not convinced of the desirability of designating possible hybrids with a binominal as though they were species. Whether or not taxonomic species have arisen in part or wholly through hybridization I am not prepared to say. I am inclined to the opinion that such cases are rare. There appear to exist in the wild certain units of the nature of species which differ from closely related groups by characters not found in these other groups; they have broad ranges which conform to known geographic areas and they have definite soil requirements; besides, these units in general behave after the manner we are accustomed to expect species to behave. There are also in some genera certain forms, usually of local or erratic distribution, which apparently show only a recombination of characters found in other units, and do not present any new characters themselves. These forms are possibly, indeed we may say probably, of hybrid origin. It certainly is confusing to designate these hybrids and also the broader group both by binomials, with no means of distinguishing one type of group from the other. For supposed hybrids I prefer to use the two parental names separated by the letter X, understanding, in the case of wild plants that the X means "a *possible* hybrid" since obviously in nature only circumstantial evidence is at hand as to parentage. It does no violence to the hybrid hypothesis that in certain groups the supposed hybrids apparently breed true and have ranges. In the Rosaceae, where many cases of this sort occur, it has been shown by Täckholm in the case of *Rosa* that apogamy often occurs. Seeds of hybrids containing apogamous embryos would naturally breed true. However, the "ranges" of these hybrids that apparently breed true do not generally coincide with geographic areas.

From the Point of View of Cytology

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Chromosome numbers may often be used to test the reliability of current taxonomic working-methods and the correctness of the results of taxonomic work.

It appears from cytologic studies that plant genera really are natural units, as the chromosome numbers of the species within a genus generally stand in clear relations to one another (they are, for instance, often multiples). As the author has tried, in another connection, to express these things, "a genus is obviously a reality, not a mere abstraction. It is a phylum of species with a common origin, as shown by the chromosome numbers that often stand in clear relations to one another. Thus, in fact, a series of multiple numbers in a genus represents a piece of evolutionary history on a small scale and may be regarded as a fairly good illustration of the monophyletic origin of such a genus." Further, the chromosome numbers of a genus often show a rather regular distribution over the different sections and species-groups. Thus, in *Carex* I have found that some sections have

low chromosome numbers, others high; in section *Montanae*, for instance, I have found the numbers 9, 15, and 19; in *Acutae* 35, about 37, 40 (2 species), and 42 (4 species). Such cyto-taxonomic interrelations show that the current sub-groups, too, of a genus generally are natural units. On the whole, studies on chromosome numbers thus tend to confirm the correctness of the results of taxonomic work in grouping the species into genera and sub-groups of genera.

Chromosome numbers are, further, of great interest in all studies on natural *hybrids*. They seem to be of quite special value in attempts to disentangle the *species* (and varieties) of *critical* groups. In many such groups, where the forms are hopelessly confused, the chromosome numbers may offer the only way of solving the problems. It should, however, be noted that this working-method has its limitations. You could prove that two forms really are different, if you happen to find a difference between them in chromosome number, but you could never prove, cytologically, that a species is a natural unit. A failure to find differences in chromosome number only leaves the whole problem unsettled; there may be great specific (genetic) differences, though the chromosome number is the same.

For further details on this question the reader is referred to the author's paper on "Chromosome number and taxonomy" in the section for cytology.

Remarks Following Professor Otto Heilborn's Paper

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I have been asked in initiating discussion of the valuable paper just read by Dr. Heilborn to call attention to the possibility of extending observations on chromosomes to other features than their association in definite numbers in a cell complex.

Chromosome number and the taxonomists' classification are not always in close agreement. This may be explained as related to such variations in chromosome number as may not affect the soma enough to afford recognition points to the systematist. Perhaps among such variations are some types of chromosome duplication involving whole or part chromosomes, or perhaps fragmentation as causing variations in number within a taxonomic group, without really adding anything to the assemblage of genes. On the other hand, forms with the same number may vary greatly from the taxonomist's standpoint.

The plants most extensively investigated from the standpoint of chromosome number are those with small, usually in meiosis rounded, chromosomes. This in part is because of the ease in counting them. In such as these there is little more that can be done at the present time in correlating genetical and cytological data. However, many other species are known which do have chromosomes with enough differences that the individuals may be recognized by constrictions, satellites, general roughness, and of course, size. In these features additional criteria of extreme value are offered. Here cases of supposed chromosomal adhesion, or of

fragmentation, may be recognized, and so such species removed from the stigma of conflict with orderly systematic grouping on a chromosomal basis. Then also cases of forms with quite different systematic position but with the same chromosome numbers may sometimes be distinguished by features of chromosome form of very great precision quite apart from relative size. This relation may operate between the taxonomists' species or between similar races within a species. Such studies have been made, and especially those currently reported by M. Navashin in *Crepis,* which appear to be extremely critical and may for the time stand as models for further studies.

The extension of cytological observations to these newer criteria will involve first a very considerable improvement in technic, which will react with advantage to cytology as a whole, for the casual methods perhaps adequate for counting are quite unsuitable here. It will involve a much greater amount of exertion on the part of the observer, for he will have to make his observations in three dimensions, and add a conception of form to that of number. Advantages will lie in a wider correlation of chromosomal, taxonomic, and genetical data, and of the morphological characters with specific chromosome types (as has already been done by Dr. Allen and Dr. Blackburn for certain degrees of sexual differentiation) so that a type of chromosome and its associated morphological characters can be recognized in different species and followed in the irregularities of mutations, crosses, etc. The result will be to render the already invaluable data derived from chromosome counts more precise, more dependable, and of wider consequence.

POINT OF VIEW OF GENETICS

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Notwithstanding the great practical difficulties presented by certain groups of plants and animals, it is unquestionably true that organisms can be with a considerable degree of success, arranged in groups to which it is convenient to apply specific names. The implications of this fact are (a) that under the conditions of habitat within which any such group is found, the range of variation does not materially transgress the limits of variation of its most nearly related (least divergent) specific groups; and (b) that either the combination of two such specific groups through cross-breeding rarely occurs, or, if it does occur, the forms arising from such cross-breeding are of such a nature as to permit their recognition as hybrids, or else their segregation products are again approximately included within the respective ranges of the parent groups.

If evolution had progressed solely or chiefly on sliding scales, as was for a time rather generally supposed, the existence of any sort of definite limits of taxonomic groups would be quite inconceivable; but the results of genetical experimentation and of accurate and extensive cytological studies have provided a mass of data bearing on the fundamental constitution of living organisms, which gives

a basis for a much clearer understanding of the nature of the limits of taxonomic groups.

To Hugo de Vries, primarily, and then to W. Johannsen, we owe the clarifying distinction between the hereditary and the non-hereditary variations of organisms, which must always be taken into account in estimating the significance of observable differences for the purposes of taxonomy. It seems useful to recognize four different kinds of variations, of which two—mutation and recombination—are hereditary, and two—induction and fluctuation—are non-hereditary. While only the first two of these might, at first sight, seem to be of importance, taxonomically, this is not the case, for it is the *relation between* the hereditary and non-hereditary variations with respect to any feature of a plant or animal which determines the availability or non-availability of that particular feature as a diagnostic character. Indeed, were it not for induction and fluctuation there could never be any transgressive variation, and every genotypic difference capable of producing a visible effect in the phenotype would serve as a basis of a taxonomic group of lower or higher grade; but the invariable presence of non-hereditary variation makes impossible the taxonomic utilization of very many quite permanent differences in genotypic constitution.

It becomes, then, a *practical necessity* to consider the nature and the amount of variation which is presented by any phenotypic character in order to determine the value of that character for systematic classification. Morphologists have long recognized that the different organs, parts and qualities of plants and animals differ greatly in their "conservatism," that is, in the relative magnitude of their variations. Internal structures which are more protected from the modifying influences of the environment usually deviate much less on each side of a normal mean than do external organs or characters. This has been the inevitable result of the regulatory mechanisms, which have necessarily developed during the progress of evolution, and which serve as "shock absorbers" to bring within the relatively narrow limits of tolerance of the living protoplasm a range of conditions of the physical environment, as of water supply, food supply, light, heat, etc., wide enough to include all of the extremes with respect to these important environmental factors, which are presented by the habitats occupied by any group of plants or animals in question, thus enabling the given organism to maintain the existence of its kind through effective reproduction and distribution.

It is owing to this difference of "conservatism" that the characters of flowers and fruits are usually more important for classification than are characters of leaves, branching habit, etc. Form, size and structure of flowers and fruits are in most cases more or less definitely related to the problem of securing effective sexual reproduction and distribution, and the regulatory mechanism which balances the mass of structures produced, against the available food supply, usually expresses itself by a *variation in number* of flowers and fruits produced, and only to a much less degree by a variation in the size of the individual flowers and fruits. I have seen, for instance, growing in tiny pockets of soil on a rocky ledge, specimens of *Lobelia syphilitica* with stems no more than five centimeters high, each bearing a

single flower of practically normal size for the species, while in rich, well-watered soil nearby were growing plants of the same species more than half a meter tall with long, densely set racemes of flowers, each flower having about the same size as that of the midget plants of the rocky ledge.

But we must turn now to the hereditary variations, as forming, of course, the fundamental basis of all valid taxonomic distinctions; on this fundamental basis the non-hereditary variations are merely superimposed with the effect of obscuring many genotypical differences and rendering them of little or no value for classificatory use, but in nowise affecting the reality or the permanence of their existence.

The intensive and extensive investigations which have been made in genetics and cytology have made it obvious that the reality of distinctions between different taxonomic forms rests almost exclusively on the reality and permanence of differences in the number and the constitutions of the chromosomes. Cytology gives us our best, and in fact, practically our only method of learning of chromosome numbers, while genetics has almost infinitely superior facilities for detecting and investigating the physiological potentialities of the individual chromosomes and of their parts. The previous speaker in this symposium has considered the cytological basis of specific distinctions and it is my rôle to discuss the bearing of genetical discoveries on the reality and permanence of the differences between different species. Numerous cytological studies have demonstrated a very widespread occurrence of differences in chromosome number in related species, indicating that change in chromosome number is a species-forming process of prime importance, while on the other hand the number of quite conspicuously distinct species whose chromosome numbers remain identical, clearly shows that changes in chromosome number, though important, are not the only, nor even the most prolific, sources of specific differences.

Mutations which produce differences of developmental potentiality in the individual chromosomes must be, therefore, the source of most of the visible differences which separate one species from another, and it is the study of the origin and distribution of these differential potentialities of the chromosomes through successive generations that constitutes the chief objective of the science of genetics.

The general results of genetical analysis of plants and animals are now so well known that it is quite superfluous at this time to go into the vast accumulation of evidence which has demonstrated: (a) that chromosomes *may*, and *generally do*, maintain their specific potentialities (genes) unchanged for very long periods of time, involving an indefinitely larger number of generations, even when they are associated successively, through the process of cross-breeding, with other chromosomes having now one set of potentialities (genes), now another, and another . . . . to whatever number of such diversely constituted chromosomes may be available within the limits of the group of forms which can successfully co-operate in sexual reproduction; (b) that when one and the same chromosome possesses two potentialities (genes) which differ from those of the homologous chromosome, one of the potentialities of the first chromosome may exchange places with the corresponding potentiality of the homologous chromosome, thus changing

the total potentiality of each chromosome without thereby changing in the least the potentialities themselves; (c) that when a given potentiality changes to a new potentiality (by gene mutation), the change takes place within a single generation—probably within a brief moment—and the new potentiality remains, thereafter, as permanent as the previous potentiality had been ; (d) that, *as a rule,* the chromosomes of different pairs assort to the two poles of the meiotic spindle quite at random, thus providing for the association in the eggs and in the sperms of all the different potentialities in as many different combinations as are represented by the mathematical permutations of the number of differentials which happen to be present; (e) that in sexual reproduction there is, *as a rule,* (but with some known exceptions) no bias in favor of the mating of some kinds of gametes in preference to other kinds; and (f) that all of the above statements are true, quite independently of the specific effects produced in the soma, by each chromosome-potentiality (gene),—whether the effect be large or small, morphological or physiological, meristic or substantive, external and seemingly trivial, or internal and seemingly fundamental.

We can see from this outline of the working of the inheritance mechanism that any group of individuals which can be distinguished by definable characters from any other group, will at any moment include within its collective hereditary constitutions a *definitely limited number of gene differences,* and that this number may be augmented by new mutational changes, and may be diminished by the accidental elimination,—or the selective elimination,—of any individual or individuals which happen to be the sole possessors of one or more of these differentiating genetic factors.

Whether a given gene mutation can serve as the basis of a taxonomic unit depends solely on the circumstance whether it produces an obvious modification of organs or characters which, owing to the limited extent of their non-hereditary variations have commended themselves to taxonomists as diagnostic characters. The gene mutation in *Bursa bursa-pastoris,* for instance, which gave rise, in nature, to *Bursa Heegeri* may be cited as an example of a gene mutation which did serve to originate an accepted taxonomic species, for in this case the character affected was the form of the seed-capsule, a character of such importance in the Cruciferae as to be usually used as a basis for distinguishing genera. Had *Bursa Heegeri* lost the power to interbreed with *B. bursa-pastoris* it would have been very properly referred to a different genus.

The great majority of gene mutations, however, do not, in their somatic effects, sufficiently overstep the range of non-hereditary variations to be utilized *singly* as the basis of taxonomic groups, or they affect only some trivial character like flower-color which has shown parallel mutations in many different species, and which for this very reason can not be used to differentiate species from one another, though they may be and often are, of sufficient definiteness to serve as the basis of groups of subspecific rank.

Genetic factors which cannot serve singly as bases for species, may, nevertheless, *collectively* produce differences of sufficient magnitude for such use, and

there is, I think, a tendency among taxonomists to prefer to recognize as species those forms which are differentiated from their nearly related species by several genetic factors. But since such groups of several factors cannot be formed or maintained under conditions of free interbreeding, the formation of valid species by such accumulation of factors involves the occurrence of barriers of some sort to free interbreeding. Such barriers may be of different kinds and of different degrees of effectiveness. They may be mechanical and absolute as in the blind gentian (*Gentiana Andrewsii*) and other cleistogamous species, or physiological and absolute as in the parthenogenetic species of *Taraxacum, Antennaria,* etc., or they may be highly effective, though not absolute, as in many self-fertilizing species, of which *Bursa bursa-pastoris* may serve as an example, the pollen being shed, in this species as in many others, in contact with the stigmas before the flowers open. Crossing may also be prevented or rendered relatively ineffective by the occurrence of various degrees of cross-incompatibility and of hybrid sterility.

In any group of organisms which freely cross-breed with each other—whether because of special contrivances which hinder self-pollination, or because of complete self-sterility, or the separation of the sexes as in dioecious plants and most species of animals, external barriers to free intercourse become of prime importance. It is not necessary to enumerate the many types of geographical barriers, but it may not be out of place to emphasize the facts (a) that what constitutes an effective barrier for one species may be no barrier at all for some other species; and (b) that while some barriers are sufficiently obvious, there can be no doubt that in a great many cases highly effective barriers exist, of which we are in complete ignorance because of the limitations of our knowledge of the physiological capacities and requirements of the given group.

The limitation of any group of organisms to a particular geographical region and to a definite series of habitats determines the extent to which inductions of one kind or another increase the range of variability. When a specific group surmounts a barrier which has previously restrained it and enters into a new set of habitats new inductions may take place, thus to a greater or less degree enlarging the total range of variation of the species, but in nowise changing it to or toward a new species. If, however, the barrier which has been passed remains as an effective barrier to interbreeding with the main body of the species which has not crossed the barrier, the new group does become a promising source of development of a new specific group, since only a unilateral and thus not a completely representative sample of the genes of the group in question are included in the individuals which have crossed the barrier, and there will now be an accumulation of unlike groups of subsequently produced genes on the two sides of the barrier. As soon as this accumulation of new gene changes, together with inductions produced by the new series of habitats, makes it possible to determine by inspection of any individual, on which side of the barrier it lived, the time has come when the new group may be recognized as a distinct taxonomic group.

Passing to the second kind of non-hereditary variations,—namely, fluctuations, —it is a well-known fact that these almost always result in a typical distribution

of the individuals to form what is known as the probable-error curve. Theoretically, this curve has an unlimited range in either direction, but there is such a relation of the frequencies at progressively greater deviations from the mean, that *practically* the limits of such fluctuating groups of individuals are fairly definite, and the continuity of the series of variations which connect the extreme members of the fluctuating group with the more populous classes near the mean, usually
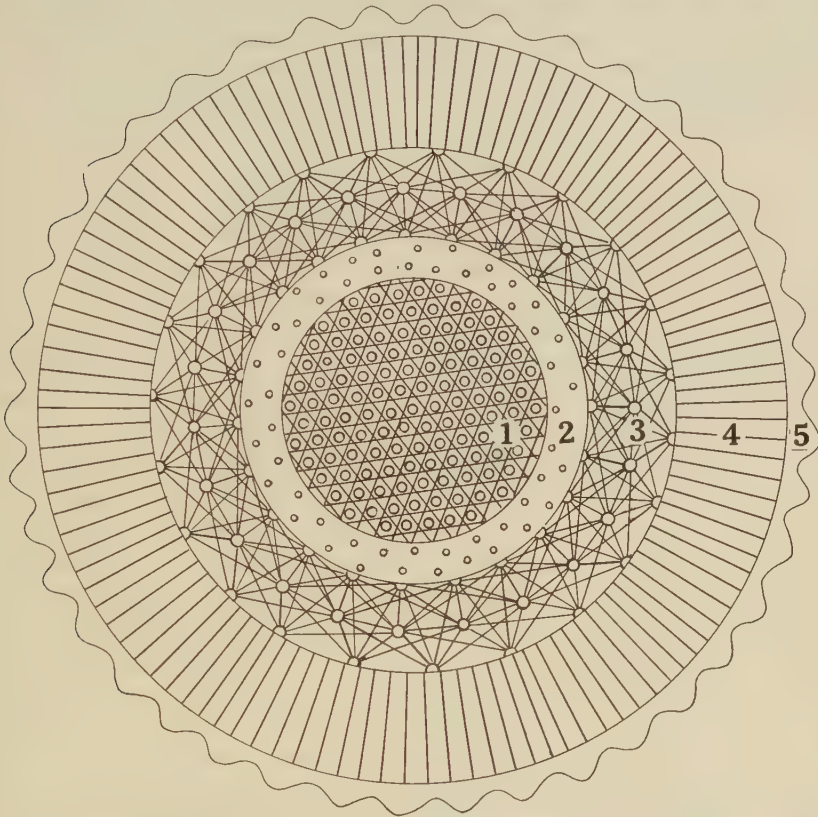
Fig. 1. Diagram to symbolize the total variability exhibited by individuals composing a freely interbreeding group of organisms. The several numbered areas have the following significance: (1) That portion of the genotype possessed in common by all individuals of the group, and therefore incapable of genetical analysis. (2) The differential genes which may be present or absent in the different individuals of the group. These are the product of gene mutations. (3) Variations produced by the various recombinations of the differential genes. (4) The inductions produced by the different environmental conditions in. the several habitats occupied by different portions of the group. (5) Fluctuating variations which are present in each single habitat.

leaves no doubt of the homogeneity of such fluctuating group. (It makes no difference from a taxonomic viewpoint that recombinations of hereditary elements (genes) are often so like fluctuations in their effects that only carefully planned and extensively prosecuted genetical experiments can certainly distinguish between them.)

It will be helpful, perhaps, to symbolize the total range of variation presented by any freely interbreeding group of plants or animals by a series of concentric circles as shown in figure 1. The inner three circles represent the sum total of genotypic elements and their recombinations and the outer two circles represent the two kinds of non-hereditary variation. Beginning at the center these concentric circles have the following significance: There is first the central disk or core (1) made up of that part of the genotype which is common to all individuals of the group and which is therefore incapable of genetical analysis. Because of our inability to analyze this common genotypic possession, it cannot be known whether it is completely or in any part composed of a group of genes similar in nature and behavior to the genes which are capable of genetical demonstration. This central core has been symbolized by Johannsen by the letters XX in his complete genotypic formulæ. The circle (2) surrounding this central "core" is intended to symbolize all the genotypic elements which may be differentially present or absent in the different individuals of the group. These and only these are capable of genetical analysis. The next circle (3) represents the sum total of all variations produced by recombinations of the several differentiating genes. Within a freely interbreeding group this circle is definitely limited to the mathematical permutations of the separable elements (genes) of circle (2). Under experimental conditions this circle may be eliminated by the establishment of pure or homozygous lines; but such artificially established homozygous lines are in no case to be considered species, but merely relatively elementary hereditary components of a species. The next circle (4) represents the various inductions ("modifications") produced by the diverse habitats occupied by the group. Under experimental conditions these inductions can be controlled to the extent of practical elimination. Finally the wavy fringe (5) surrounding the whole figure represents the fluctuations such as occur within the single habitat and which cannot be experimentally eliminated. The figure as a whole represents a succession of limiting conditions which indicate that, as viewed from the standpoint of genetics, the ranges of variation of such freely interbreeding groups are definite and natural.

If we compare with this the condition in a parthenogenetic species, or one which is reproduced by some other asexual method, or which is practically limited to self-fertilization as its method of reproduction, we find the situation considerably simplified in one respect, but complicated in another, for here circle 3 is eliminated and circle 2 may be reduced or likewise eliminated, leaving only the central "core" surrounded by the circles (4 and 5) representing the non-hereditary variations (induction and fluctuation). Each such group of individuals constitutes a distinct biotype, and could under some conceivable circumstances likewise be properly recognized as a species. But far more commonly the taxonomic species is made up of a mixture of several biotypes which cannot be successfully distinguished by inspection alone because of the extensive over-lapping of their inductions and fluctuations. In figure 2 is represented the relations of three biotypes of a single taxonomic species. The limits of variability of a group thus constituted are coincident at every point with the limits of variability of some one or more of the in-

cluded biotypes and are, taken point by point, just as definite and natural as are the limits of variability of each of the component biotypes, but the naturalness of the group *as a whole* depends upon the ability of the student to so define it that it will include all the individuals of a certain series of biotypes while excluding the individuals of all other biotypes. There is no doubt that the grouping of biotypes in nature is such that this can be in many cases successfully approximated, while in many other cases it can not be successfully done. It is for this reason that species sometimes represent natural groups, in other cases only quasi-natural groups, and in the latter case it is inevitable that different taxonomists should differ in their individual judgments as to where specific limits can be practicably drawn.
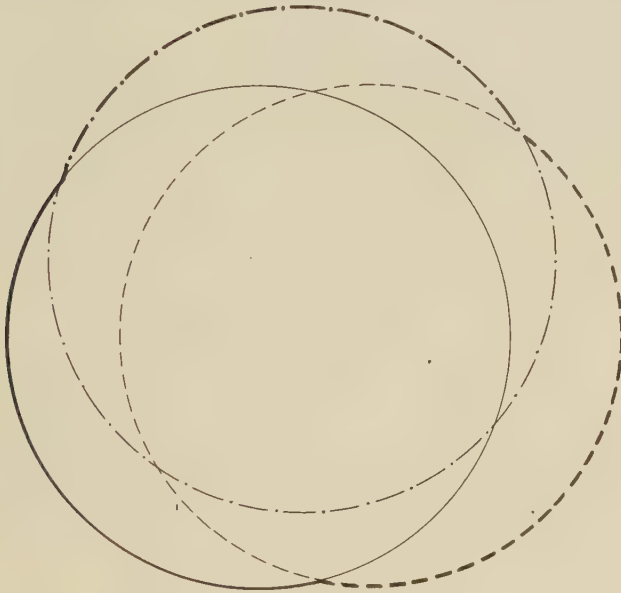
Fig. 2. Diagram to illustrate the relations of several biotypes of a non-interbreeding group of organisms. These biotypes are, individually, natural entities, but because of extensive overlapping they must be included in a single taxonomic group. The limits of such a species are in each direction definite, but in different directions they may be determined by the limits of different biotypes.

As the geneticist sees the situation, *innumerable natural lines of cleavage traverse the fields of living organisms,* and these lines are generally capable of discovery by the application of appropriate experimental methods, but many of these natural lines of cleavage are unavailable for taxonomic use among organisms which must be grouped solely on the basis of the phenotypic morphological characteristics which they exhibit. If it is desired to make taxonomic distinctions more natural, it will be necessary to resort more and more to experimental methods. The application of experimental methods to taxonomy has reached its highest development in the field of bacteriology, where specific identity is determined by the introduction of individual clones into a series of standardized environments, known as "culture

media." Alexis Jordan about the middle of the last century introduced a somewhat similar method into the taxonomic study of macroscopic plants. He established a private experimental garden into which he brought plants whose taxonomic position he wished to learn, and in this way he discovered many natural groups (biotypes) of plants of whose existence other taxonomists of his day were completely ignorant. Many other taxonomists have since made minor use of this method, but the method seems to commend itself for more general use. Why should there not be *gardens for experimental taxonomy* established at every institution in which research in taxonomy is in progress? The utilization of genetical methods in the study of taxonomy have already made notable contributions toward an understanding of relationships in certain great and difficult groups of plants. I need mention only several examples, such as W. O. Focke's studies of *Rubus*, Brainerd's work with *Viola*, Sargent's with *Crataegus*, and Täckholm's and Hurst's with *Rosa*, to indicate how greatly a more extensive adoption of experimental methods would deepen and strengthen the work of the taxonomist by leading him to the discovery of natural relationships which mere superficial inspection, however carefully it may be done, could never discover.

Discussion of Dr. G. H. Shull's Paper

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The difficulties that present themselves in attempts to limit and define taxonomic units have very greatly increased with the development of genetics and the practices of genetical experimentation. Assemblages that seemed fairly satisfactory species in the older manuals have broken up on genetical analysis into smaller groups which are unquestionably biological units maintaining their characteristics when isolated and bred in the experimental garden. The analyses of the experimental garden may be carried to so fine a point that biotypes are established which differ from one another by only one character or by a single group of characters that hold together through linkage. Cytology supports these findings of genetics with clear evidence that characters are expressed through specific chromosone structure and by particular chromosome associations. For the geneticist these biotypes are units which must be considered in any attempt to construct a full system of classification.

Yet no geneticist is likely to insist that taxonomy follow to the end the findings of genetics and cytology, for the obvious reason that such detail would kill interest in taxonomy by the weight of its data. The problem would seem to be one of adjustment. Let there be at least for those who love Nature in a large way a type of manual that stresses relationships by the assembling of forms in larger groups rather than their separation by a splitting so fine that relationships are hidden through the detail presented. The conception of a collective species has very clear advantages for taxonomy of this character and should not be discarded.

For the taxonomy that studies a group intensively hoping to learn something

of the evolution of its species the findings of genetics and cytology cannot fail to be of significance. They are likely to prove of especial value at critical points in the problems of interpretation. It is a matter of particular satisfaction that when cytology and genetics have been brought together on a problem they have either given mutual support through agreement on conclusions or they have taken positions so far apart as to show at once that appearances did not truthfully express the real situation.

These points may be illustrated by the taxonomic problems presented in the genus *Oenothera*. Studies of material assembled and grown in experimental gardens have shown that there are very many more species than are given in the manuals. Genetical and cytological studies, well worked out for certain forms, indicate that most of the species in the genus are impure or heterozygous, breeding fairly true, however, because for the most part only those gametes live or produce viable seed as will reproduce the heterozygous parents. Most of the germinal variations in the genus are apparently either forms of segregation expressed through recessives set free by the elimination of lethals, or they are variants resulting from unusual chromosome associations which occasionally produce marked sports. That species of Linnaeus, *Oenothera biennis*, refers to a definite plant, the early history of which in Europe is remarkably clear, and in recent years the cytology and breeding behavior have become well known. We can no longer treat *biennis* as a collective species, as American floras at present do. As a matter of fact, *biennis* is rare with us and American herbaria have assembled under this name material of a number of different species some of which have been isolated through genetical studies. *Oenothera* is a genus in which taxonomy must bow to the findings of genetics and cytology and radically revise its treatment of certain species, but it cannot be expected, at least in the manuals, to present more than the most important of the species that future investigations may determine. A manual can, however, at least call attention to the fact that a genus contains numerous species, distinguished by small but constant characters, and give some suggestion of the interest that may attach to the group through genetical studies.

As illustrating another type of genetical and cytological analysis which taxonomy must recognize should be mentioned the brilliant work on polyploidy which is so rapidly coming to the front. These studies on wheat, roses, *Hieracium*, crysanthemums, *Carex*, *Rubus*, *Crataegus*, etc. are demonstrating relationships among species and indicating methods of evolution of exceeding interest because of the system displayed. We are obtaining information on surprisingly exact mechanisms and definite behaviors which bring to the problem of the origin of species much of satisfaction. Taxonomy must take note of such work and make use of its conclusions.

The geneticist and cytologist obtaining their results with much patience and labor seem justified in asking the taxonomist to proceed slowly with his publication, at least in groups where it is clear that genetics and cytology may be of material assistance in establishing relationships. The future of taxonomy obviously will offer less of the pioneer work of exploration with its chief aim the description of new

species. In its place will come intensive studies on particular groups, a type of work that must be keenly analytical and to which genetics through the experimental garden may make material contributions.

The taxonomic unit must rest on a basis of relationship, judged by whatever evidence is available. Whether the units be larger or smaller is sure to be determined in large measure by the attitude of the individual investigator, his point of view, and his aim in publishing. We shall always have with us the conservative and the radical, the one seeking relationships and hesitant to describe new species, the other impressed by diversification and anxious to record his findings.

GENERAL DISCUSSION

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I presume we all agree that taxonomic units, large or small, should be groups of "blood relatives." A natural classification finds its best basis in phylogeny. Furthermore, no one denies that a classification of plants or animals should bring to expression as adequately as possible the knowledge available as to the evolutionary history of living organisms upon the earth.

The question naturally arises whether the binominal nomenclature and the rules of naming as at present developed are adequate for the new situation. We find here two groups of workers with somewhat divergent viewpoints: First, there are those who are most concerned with bringing into orderly and relatively permanent groupings the mass of plant names and the descriptive knowledge of the plants themselves which have come down to us from the labors of the botanists of the past. Second, we have those primarily concerned with the adequate naming and classifying of the vast mass of new material resulting from the more intensive study of plants in the field; likewise, new material is continually being brought to light by the methods of genetical experiment and analysis and by the practical work of horticulturists and plant breeders.

We must not forget how largely Darwinian evolution was based on a study of horticultural and zoöcultural materials. Present-day genetics and cytology also have found their materials to a large degree in the products of plant and animal breeding, ready at hand for more refined and critical analysis by laboratory methods. I think we should all admit that we are just beginning this analysis. It is natural, then, that the practical questions lying back of this symposium concern largely the adequacy of the existing taxonomic units and the recognized methods of grouping them to bring into orderly relations the vast accumulation of new material, which closer study and experimental methods have added to the already existing mass of horticultural and natural types. No ready-made answer to these questions is probably to be expected.

It is highly interesting that, with the discovery of this vast mass of new material, nothing has been brought to light which suggests other than a phylogenetic basis for a natural classification, but when we consider the feasibility of attempting

to indicate such relationships in the arrangement of genera, species within the genus, and varieties, races, pure lines, mutants, etc. within the species, we are confronted with serious difficulties and wide divergences in practice. To turn to some very concrete points, I cannot help feeling that the nomenclatorial type concept has contributed in a way to increasing this confusion in practice, especially when emphasis upon the recognition of nomenclatorial types is allowed to crowd the attempt to identify biological types into the background. That the biologically highly significant word *type,* with all its evolutionary connotations, has become associated with the matter of merely nomenclatorial identity can hardly be regarded as other than unfortunate. There should be in this day no possibility of disagreement among evolutionists that the type specimen of a species and the type species of a genus should be in each case respectively, so far as determinable, the biologically typical specimen and the biologically typical species. No mere accidents of discovery and formal naming should be allowed to obscure in any way the fullest possible expression of our evolutionary concepts in our taxonomic groups, whether large or small. It is urged that such aims are chimerical, or at least impractical, but it is, in my opinion, questionable whether morphology and taxonomy can afford to encumber themselves with such artificialities, reminiscent of pre-Darwinian principles of classification, as are the nomenclatorial type conceptions.

Granting, of course, that natural keys are not always or completely possible, a second source of confusion, in my opinion, is the widespread use and acceptance of artificial keys. Again, the argument is the practical one. A key should lead by the most direct and unmistakable route to a name. For the beginner, with an instinct for classifying, is it as important that the route be short as that it be interesting and instructive? And for the practised morphologist or systematist who knows his groups, is speed a fair equivalent for irritation at artificiality?

To turn again to the more general viewpoint, this much is obvious: The papers on this program show clearly that the alliance between genetics and cytology is already fruitful and gives rich promise for the future. Taxonomy and the new experimental plant geography have joined this alliance and are subjecting the natural races and varieties, under the experimental conditions of field stations, to the methods of analysis worked out in the genetical and cytological laboratories.

There is need today, in my opinion, for the work of trained systematists to bring into orderly form the great mass of horticultural material already available as well as the flood of new types produced by experimental and analytical breeding methods.

THE DELIMITATION OF SPECIES OF FUNGI ON PHYSIOLOGICAL GROUNDS[1]

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Mycologists who are accustomed to the study of those fungi that are obligate parasites—the rusts, powdery mildews, many of the downy mildews, and so on— know how great is the temptation, and how frequently it is yielded to, to distinguish species by their ability to attack particular host plants and their inability to grow on others, rather than by any morphological character.

Those too who have worked extensively with cultures of fungi on artificial media, who have studied groups in which cultural characters have come to be given importance in classification, know equally how common it is to found species on some particular growth character or even on biological peculiarities, such as capacity for fermenting certain sugars, discoloring certain media, and the like.

Examples of these tendencies are easily given and could be multiplied. The study of the rust fungi has developed almost from the beginning with the tendency, strongly marked, to distinguish species according to their hosts. When a rust is found on a particular host, search is made amongst the species of the genus already recorded on the same host, or perhaps on a few allied species, and if none is found to agree, it is frequently regarded there and then as a new species. Indeed Fischer in "Die Uredineen der Schweiz" regards all rusts as distinct if they differ in the genus of plants to which they are restricted. In many cases in which a species was originally described as occurring on a number of hosts, there has been a disposition to separate it into several species each confined to a particular host genus (for example, *Puccinia rubigo-vera*, *P. lolii*, *Uromyces trifolii*). A further step has been attempted: when a species has a number of strains confined to different varieties of the same host plant, for example, *Puccinia graminis* on wheat, suggestions have been made to split it into several species, some of which would have somewhat distinct morphological characters.

In the smuts the distinction by hosts is almost complete. In spite of the fact that one was aware in a general way that *Ustilago tritici* and *U. nuda* were morphologically similar, it comes as a surprise when one finds the loose smuts of wheat and barley united into a single species *U. tritici*, as Cunningham ('24) has done in his recent monographic treatment of the smuts of New Zealand.

The Erysiphaceae as dealt with in Salmon's monograph ('00) form a good expression of the opposite tendency to that which has been shown on the whole

1590

in the rusts and smuts. The 160 species that are recorded in Saccardo's "Sylloge" as having been named up to that date were reduced to 49 and 11 varieties, in spite of the fact, established largely by Salmon himself, but also by Neger and Marchal, that many of these species contain specialized forms restricted to one or a few hosts. Though Blumer ('21–'25) has shown that certain of these forms can be distinguished by morphological characters, the size of the conidia differing on different hosts, he has been cautious in giving specific rank to any but rather extreme cases. Jørstad ('25) in his recent monograph of Norwegian Erysiphaceae follows Salmon, except that certain of the latter's varieties are considered to be distinct species. A study of the synonymy, and of the range of the characters on the different hosts and their gradation into one another, as set out in Salmon's monograph, shows clearly the disadvantage that would result, in this group at least, from distinguishing the species according to the hosts on which they occur.

Coming to the downy mildews, the genus *Peronospora*, as represented in Saccardo up to 1910, contained 113 species, a good many of which were probably synonyms. Gäumann's monograph ('23) lists 267, of which 146 have Gäumann's name attached. The single species formerly recognized as a crucifer parasite, *P. parasitica* (Pers.) Fr. is divided into 54, of which only five were recognized by any earlier writer as having specific rank. These are not distinguished by oospore characters, nor can they be recognized by those of the conidiophore, since of the 15 types of the latter distinguished by the author, all intermediate stages can be traced. A biometrical study of the conidial dimensions shows that, while each of Gäumann's species differs to some extent from the others, the peak of the curves for length and breadth gives only a fraction of a micron difference in many cases, while the quotient of length by breadth is identical or very close also in many cases, giving, for instance $1 \cdot 16$ in five, $1 \cdot 15$ in four, $1 \cdot 14$ in four, and so on. Since the age of the conidia affects this figure, as well as the other data, it is evident that little can be gained by attempting to separate the species on this basis. From these morphological characters alone, Gäumann ('16–'18) considers that one can do no more than place a given example of the genus in the "collective species" to which it belongs, in this case *P. parasitica* of the older authors, further separation into the individual species requiring, as the only constant and indisputable means of distinction, a determination of the physiological selection of host plants. It is only on this last basis that his 54 species can be identified, for though in the diagnosis of each the morphological characters are also given, it is evident that without knowledge of the host, identification would be impossible in a large proportion of them. How widely this conception departs from that in Salmon's Erysiphaceae is at once evident. If generally accepted, it would be difficult to deny specific rank to the numerous races of the fungus still usually known as *Puccinia graminis*. That it is not likely to be generally accepted, even in his own country, is evident from Fischer's ('17) correlation of Gäumann's forms with Johannsen's pure lines of beans, and his relegation of them to the group of "kleine Arten" or "formae speciales."

If we turn to the fungi that have been critically studied in artificial cultures, whether facultative parasites or merely saprophytes, we find a similar diversity

of outlook. Westling's monograph ('11) of the green species of *Penicillium* is stated by the author to be a critical study on a morphological basis. Thom also has maintained, on the whole, a morphological criterion for his species. Both attach a certain weight to physiological characters and both insist that the morphological characters should be studied on uniform media. But, as Westling says, from this standpoint to one in which physiological data are given a dominant position in the diagnosis of species is all too great a step. Biourge ('23), dividing the genus on growth characters, has multiplied species in a manner that recalls Gäumann. He states that whereas Saccardo in 1900 had listed only 42 species, with 2 *Citromyces* (now included in *Penicillium*), he himself found over 290 names in existence in literature. In his monograph he accepts 128 species and admits that he has not been able to recognize in his cultures many of the species described by others. Even in the division of his sections he makes use of cultural characters, such as zonation in Petri dish cultures, and, though his species have diagnoses including morphological characters, it is probable that it would be impossible to determine many of them by these alone, without the extensive series of cultural tests that are appended in each case. Like his predecessor Dierckx, cultural characters are given greatest weight, and of the latter's handling of the genus Lindau ('07–'10) remarks: "This does not make for clearness, but only increases the confusion."

An extreme case of the use of biological characters in classification is presented by the genus *Monilia* as recognized by medical workers. Castellani's ('25) method of distinguishing species of these fungi is based primarily on their fermentation of a series of sugars, since, as he puts it, morphological grounds do not suffice for a classification. In the genus *Beauveria*, including the fungi parasitic on insects formerly known as *Sporotrichum globuliferum*, *Botrytis bassiana*, etc., attempts have been made to separate species by the color they impart to various culture media. As might be anticipated, recent studies by Petch ('26) have shown that this character is inconstant and cannot be relied on. Precisely the same thing is happening in regard to the color and other cultural characters used in the diagnosis of the ringworm fungi, as a result of studies of large numbers of isolations.

Fungi that belong to what are sometimes known as the hemi-saprophytes, that is, species mainly parasitic but capable of a saprophytic life and, therefore, culturable artificially, present several examples of the difficulties of the systematist. The section *elegans* of the genus *Fusarium* contains a number of vascular parasites of all kinds of herbaceous and shrubby plants. In Erwin F. Smith's ('99) classical study of the forms causing wilt of cotton, watermelon, and cowpea, those on the two latter hosts were regarded as varieties of that on the first, on the ground apparently that each was restricted to particular hosts, since it is definitely stated that all are morphologically identical. Other varieties were subsequently added, for example, *F. vasinfectum* var. *pisi*, the cause of the "St. Johanniskrankheit" of the pea in Europe. Later on all these have been given specific rank. If now one examines the morphological characters of many of these *elegans* forms, as shown in Wollenweber's "Fusaria autographice delineata," one

is forced to admit that Smith's earlier view was justified, since the variations shown in the five plates of *F. orthoceras* are greater than the differences between, say, *vasinfectum*, *tracheiphilum*, *niveum*, *oxysporum*, *hyperoxysporum*, and *cubense*. In regard to the last of these, the cause of the Panama disease of bananas, both Brandes and Wollenweber state that it is scarcely different from *F. vasinfectum*. I have had three of these vascular parasites under study in India, the causes of wilt diseases of pigeon pea, cotton, and sesamum. I described ('10) the former as a new species, *F. udum*, mainly on cultural characters. Subsequently I considered the cotton wilt producer of India as distinct both from *F. udum* and from the cause of cotton wilt in America *F. vasinfectum*. Recent comparative study of the sesamum fungus and of *F. cubense* has failed to show any morphological differences, and the cultural differences that were earlier noted in the case of the other two, both between themselves and from *F. vasinfectum*, have broken down. Even the biological character of host specialization appears to be less fixed than had been believed. Small ('22) found in Uganda a fungus morphologically and physiologically identical with *F. udum* but capable of attacking many other plants besides pigeon pea. Similarly *F. cubense*, as it occurs in the Caribbean, cannot infect *Musa cavendishii*, but a morphologically identical fungus causes a wilt of this species of banana, indistinguishable from Panama disease, in the Canaries. And in Egypt Fahmy (according to letters received from him) has under study three strains of cotton wilt-producing fungi of the *F. vasinfectum* type, one from America which mostly attacks American varieties; one from India restricted to Indian cottons; and one from Egypt chiefly on the Egyptian. Morphological differences between the three strains are very slight, but there are cultural differences. If specilization of parasitism is the guide, there would seem to be as good reason for giving specific rank to the Indian strain, which refuses to attack Egyptian cottons, as to most other species in the *elegans* section, but what is to be done with the Egyptian strain which sometimes attacks the Indian varieties?

In all these cases the problem resolves itself into one of the relative weight to be attached to a certain group of physiological characters in classification. The same general set of physiological characters is responsible for the ability or inability of an obligate parasite to grow on a particular host plant as for a saprophyte to show certain characters in artificial culture. It is largely a question of being able to use particular nutrient materials or of being able to alter substances by enzyme action so that they may be assimilated or at least neutralized. It appears to be extremely doubtful if any more weight should be attached to host specialization in the parasites than to cultural characters in the saprophytes, and if we refuse to except the one in classification it is difficult to justify the use of the other.

There are, indeed, quite evident signs of a revolt against the subdivision of species on biological characters. Thus Cunningham ('23) wishes not only to unite *Ustilago tritici* and *U. nuda*, as mentioned above, but also to restore the old species *Puccinia elymi* to include *P. triticina* with several other rusts now regarded as distinct, and Mains and Jackson ('26) have recently indicated their

sympathy with such a view, while doubting the expediency of altering what has become established usage. Hansford ('25) has argued that the present classification of species in the *elegans* section of *Fusarium* is useless and that it is preferable to regard all those, at least, that he has studied (including quite a large number ordinarily recognised as distinct) as strains of a single species. Small, in a recent study of strains of the genus *Colletotrichum* in Uganda ('26), considers that nearly all those he has encountered on various hosts are but forms of a single morphological species.

We can recognise three distinct tendencies in the classification of fungi of the types under consideration. The older, purely morphological one, as defined by Marshall Ward ('05) who considered that "no species can be accepted as valid until it is capable of definition in morphological terms," a view which is being reverted to by some at the present time; the almost purely biological, as instanced by Gäumann's treatment of *Peronospora*; and that in which both morphology and physiology are taken into account. Is there any direction in which guidance can be sought as to which of these tendencies may best be followed? I think that such guidance can be found in certain evolutionary considerations.

In his presidential address to the Zoology Section of the British Association last year, Regan defined a species as a community or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it or them to specific rank. No rule is required for the guidance of the systematist in this; convenience may often be the best criterion. He illustrates with a number of striking cases, the view that throughout the evolution of the fishes, changes of structure have been intimately related to, and may even be said to have been determined by, changes of habits. The importance still given to adaptive factors in evolution by competent biologists, as illustrated in this case and also in H. F. Osborn's opening address to the same section in Oxford, ten or twelve days ago, may make us more ready to admit that the mere colonizing of a new host plant by a rust or mildew may lead not only to special biological characters but also to some morphological changes, which may become in time, no matter by what agency, permanent. How else can we explain the slight morphological differences so often noticed in biological races?[2] It is obvious that a stage may arise when it becomes a question whether such adaptive modifications are of sufficient magnitude to justify specific rank. It is here that the "competent systematist" appealed to by Regan has his field. It is assumed that he has a knowledge of the allied species and perhaps an inkling of the form from which they have been derived. Without this, his opinion is valueless. With it, he may say, for instance, that all the races of black rust are sufficiently like each other, and sufficiently different from other rusts,

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[2] The absence of a previous host plant, as must often occur when a plurivorous species spreads to a new area, might have a similar influence. Fischer ('13) found a form of *Uromyces caryophyllinus* that in the Wallis (Switzerland) region infected *Saponaria ocymoides* and *Tunica prolifera*, whereas when collected in Baden, where *S. ocymoides* is absent, the spores had lost the power to infect this plant, though *Tunica* was readily attacked. It is, no doubt, in some such way that Fahmy's strains of *Fusarium vasinfectum* originated.

whether those that occur on the same host plants or elsewhere, to be kept within the species *Puccinia graminis*. He may consider that all the downy mildews on the Cruciferae are sufficiently alike to be included in *Peronospora parasitica* or a few (a very few, I think) can be readily recognised and may be regarded as different species. If there were no large range of intermediate forms, as may come about by the suppression of some, it might often be preferable to recognise several species in an allied group. Regan points out that if there were only Englishmen and Hottentots we would probably speak of two species of man. From the evolutionary standpoint it is often a matter of convenience where we draw the specific line, and convenience demands generally a morphological criterion, since it is obviously not convenient to the taxonomist to have to carry out an extensive series of experiments before the proper pigeon hole into which to put an organism can be found. The cerealist or phytopathologist who wishes to know exactly what strain of rust he handles, or the physician in dealing with the ringworm fungi may require to do this, and it may be left to them, as it is left to the agronomist or horticulturist to know the cultivated varieties of the plants with which they deal.

Furthermore, and this applies almost as much to the biological races as to the saprophytes with cultural strains, adaptive characters are liable to fluctuate rather freely, perhaps as a result of changes in the environment. Hosts that are resistant under one set of conditions may become susceptible under another. Even a variation of temperature may sometimes break down resistance to infection, as shown at Madison and elsewhere, and it must not be forgotten that for a parasite the host plant constitutes a large part of its environment. The forms of *Fusarium vasinfectum* in America, India, and Egypt and of *F. cubense* in the West Indies and Canaries might not maintain their host specialization under modified conditions. I do not understand how they could have come into being without plasticity of some sort. Saltants are now known to differ at times from the parent strain in virulence, and there are various way in which a fungus might change its host range. Hence it is difficult to admit that biological specialization alone is a sufficient basis for distinguishing species unless one is prepared to face a large number of cases in which this criterion will not serve.

Still less in the case of moulds like *Penicillium* can cultural characters be given specific weight, though they may bring support to morphological differences. Color and type of growth (aerial mycelium, formation of coremia, pionnotes, etc.) are two characters much used in the cultural identification of species, but they are unstable characters, like most of the others of this category. It is possible to "stretch" the cultural characters of a group of strains of a single organism, such as *Fusarium blackmani*, by controlled modifications of the medium on which they are grown, as has been shown by Brown and Horne ('25–'26). The amount of aerial mycelium, rate of growth, zonation, color, amount of sporulation, septation, and even to some extent size and shape of the spore, can be made such that, if constant, they would denote distinct species; yet all can be derived from a monospore or single hyphal tip culture, intermediate forms exist, and each can be made to resemble the other. F. L. Stevens

('22) dealing with a similar case in the genus *Helminthosporium* points out that it would be possible by biometrical, biological, and cultural criteria to draw up distinctive diagnoses for a number of the races he studied, but he prefers to regard at least the great majority as falling within the Linnean species, *H. sativum*. In some cases it would appear that morphologically good species, readily recognisable as such in nature, can be "stretched" in culture so as to overlap one another. The writer believes that this has occurred in Leonian's ('25) recent cultural study of most of the described species of *Phytophthora*, where some 24 species and strains were united into *P. omnivora*. Cultural study here has led to the view that the size and shape of the fruiting bodies are minor characters, but some, at least, of these fungi can readily be identified as they occur in nature and, indeed, in culture, and if this is so it is a strong argument for keeping them distinct.

Considering these and similar cases in the light of convenience, it appears that it may sometimes be preferable to unite and sometimes to divide. It may be convenient for practical reasons to keep *Ustilago tritici* and *U. nuda* distinct. *Colletotrichum limetticolum* is probably, as Burger ('21) holds, merely a strain of the ubiquitous *C. gloeosporioides*, but it causes the destructive withertip disease of limes, whereas the common forms of *C. gloeosporioides* on *Citrus* are, at most, weakly parasitic, and so it may be kept apart. The disadvantages of multiplying species are so many, however, that we would probably be well advised to regard such cases as entirely exceptional.

If we admit that there is no such thing in nature as a pure, invariable, homogeneous species, that habit can modify the facies of a species so long as it endures, that morphological characters are less readily modified by the environment than physiological, and that convenience is often the best guide where to draw the line between different species, we may get some degree of guidance as to which of the tendencies defined above may best be followed. We will be led, I think, on the whole to prefer the morphological basis of classification and only in special cases to stress biological differences.

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CLASSIFICATION OF SPECIES OF CORTICIUM BY THE TISSUES OF THE FRUCTIFICATION[1]

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In the several parts of my work, The North American Thelephoraceae, I have incorporated into the descriptions of the species details of the tissues of the fructifications whenever such matter was useful in recognition of the species. In bringing this work to a conclusion with the genus *Corticium*, the tissues have proved especially helpful, for there is a large degree of constancy in the characters of these tissues for the same species.

The fructifications of *Corticium* are always resupinate and have the appearence of a coat of paint on the surface of some substratum, which is usually of wood or bark. One hundred and six species of *Corticium* are recognized in my work as occurring in North America and the outlying islands. It does not seem probably that the determination of more than a very few of these species can ever be by inspection of their external characters.

The tissues of many of these species remain hyaline or so nearly so during their whole existence that no appreciable color can be detected when the fructification is viewed in vertical section. In other species the tissues produce pigment by which some tissues or all the tissues are so loaded or colored that the fructification is perceptibly colored when viewed in section. Such color observations are readily made by inspection of the fructification when cut through from upper to under side and confirmed by examination with the microscope of thin vertical sections of the fructification. At the same time these sections show also whether gloeocystidia or other noteworthy differentiations of tissue, other than basidia, are present.

Upon the bases of absence or presence of color of the substance, that is, tissues, our species fall into three primary groups, of which about half are in group I., with substance not appreciably colored and lacking gloeocystidia. Group I. is immediately subdivided into two minor, nearly equal groups upon the basis of whether the hymenium is white or colored. The advantage of this primary grouping is that it is important for a usable scheme of classification for so large a body of species to combine, if possible, ease of application with a high degree of accuracy in the final results.

The exact details of the above grouping and its further divisions are shown in the following Key to the Species, which is now in course of publication in the Annals of the Missouri Botanical Garden 13: 173–340. 1926. The publisher has

very kindly struck off advance copies of the Key to the Species for our use on the present occasion. In this Key, our species are designated by numbers from 1 to 107. A list of the species under their respective serial numbers is given to supplement the Key.

KEY TO THE SPECIES

I. Substance not appreciably colored, no gloeocystidia.
    1. Hymenium white or whitish when growing.............................. *1–23*
        *With antler-shaped paraphyses or color change from yellow to white in fruiting *1, 2*
      **Spores globose or subglobose.
        a. Imbedded spores (chlamydospores) usually present.................. *3, 4*
        b. Imbedded spores not yet observed............................... *5–9*
     ***Spores more elongated.
        a. Spores large, more than 6μ long.....................................*10, 11, 33*
        b. Spores small, hypahe incrusted or among obscuring mineral matter..... *12–16*
        c. Spores small, hyphae not incrusted................................ *15–23*
    2. Hymenium colored when dry and not known to be white at first—usually some
        shade of buff, yellow, red, brown or blue...:.......................... *24–56*
     *Spores globose or subglobose, less than 5μ in diameter...................... *24–26*
     **Spores globose or subglobose, more than 5μ in diameter................... *27–29*
     ***Spores more elongated.
        a. Spores very large, 10–18μ long................................... *30, 31*
        b. Spores large, 6–12μ long...*32–44, 90*
        c. Spores small, hyphae somewhat incrusted...........................*12, 45–48*
        d. Spores small, hyphae not incrusted, fructifications separable........... *49*
        e. Spores small, hyphae not incrusted, fructifications closely adnate or only
            small pieces separable.. *50–56*
II. Gloeocystidia present or structure vesicular, or some tissue noteworthy, substance
    colored or not colored.
    *Gloeocystidia present or shown by vesicular structure or by colored, resinous-
      appearing masses...*57–86, 107*
        a. Gloeocystidia not colored, elongated; imbedded spores numerous......... *57–58*
        b. Gloeocystidia not colored, elongated, lacking chlamydospores.
          †Spores globose, subglobose or broadly ovoid.......................... *59–66*
          ††Spores more elongated...*66–71, 79*
        c. Gloeocystidia not colored, pyriform to globose........................ *72–79*
        d. Gloeocystidia colored, elongated...................................... *80–83*
        e. Gloeocystidia colored, subangular or globose, resinous-appearing..........*66, 84–86*
    **Distinguished by antler-shaped branching of some hyphae or paraphyses, or other
      branching of paraphyses, or unusual form of other tissues....................
       ....*1, 17, 23, 29, 36, 38–40, 60, 72, 76, 80, 87, 88, 92–94, 107*
    ***Numerous imbedded spores or other than basidiospores.................*3, 4, 11, 37, 57, 58*
    ****Spores green, even... *105*
    ******Spores usually white but finally becoming ochraceous......................... *34*
III. Substance colored, no gloeocystidia...................................... *87–106*
    *Fructifications ranging from gray to drab.
        a. With paraphyses having slender branches; spores small.................. *87, 88*
        b. Paraphyses not noteworthy; spores larger, 7–10μ long.................. *89–91*
    **Fructifications ochraceous to wax-yellow and red.
        a. With some hyphae or paraphyses having antler-shaped or racemose branch-
          ing.. *92–94*
        b. Tissues not having antler-shaped or racemose branching................ *2, 95–99*

***Fructifications darker, tending to brown and vinaceous.
    a. Parasitic species.. *100–102*
    b. Always saprophytic.. *103, 104*
****Fructifications green or blue... *105, 106*

List of Species of Corticium

1. C. paraphysatum
2. C. sulphureum
3. C. punctulatum
4. C. vellereum
5. C. granulare
6. C. ermineum
7. C. Berkeleyi
8. C. arachnoideum
9. C. portentosum
10. C. bombycinum
11. C. sociatum
12. C. scutellare
13. C. tuberculatum
14. C. crustaceum
15. C. pelliculare
16. C. Auberianum
17. C. galactinum
18. C. calceum
19. C. vescum
20. C. incanum
21. C. canum
22. C. centrifugum
23. C. Atkinsonii
24. C. subnullum
25. C. crustulimum
26. C. tessulatum
27. C. Stevensonii
28. C. lacteum
29. C. subgiganteum
30. C. ceraceum
31. C. Bambusae
32. C. cremoricolor
33. C. confluens
34. Coniophora corrugis
35. C. laetum
36. C. roseum
37. C. salmonicolor
38. C. spretum
39. C. rubropallens
40. C. rubrocanum
41. C. cultum
42. C. rubellum
43. C. hydnans
44. C. rubicundum
45. C. granulatum
46. C. illaqueatum
47. C. Rosae
48. C. apiculatum
49. C. subceraceum
50. C. roseo-pallens
51. C. ochraceum
52. C. furfuraceum
53. C. lividum
54. C. Overholtsii
55. C. Pseudotsugae
56. C. confine
57. C. analogum
58. C. effuscatum
59. C. abeuns
60. C. ravum
61. C. mexicanum
62. C. epigaeum
63. C. lactescens
64. C. salmoneum
65. C. Macounii
66. C. argentatum
67. C. septentrionale
68. C. stramineum
69. C. Litschaueri
70. C. protrusum
71. C. livido-caeruleum
72. C. pilosum
73. C. radiosum
74. C. vesiculosum
75. C. globosum
76. C. sulbalbum
77. C. vinososcabens
78. C. polygonium
79. C. chrysocreas
80. C. involucrum
81. C. luridum
82. C. jamaicense
83. C. debile
84. C. venosum
85. C. ochrofarctum
86. C. Tsugae
107. C. paniculatum
87. C. subcinereum
88. C. albido-carneum
89. C. adhaesum
90. C. leptaleum
91. C. laeve
92. C. investiens
93. C. pectinatum
94. C. racemosum
95. C. subcontinuum
96. C. Murrilli
97. C. subochraceum
98. C. canadense
99. C. bicolor
100. C. koleroga
101. C. Stevensii
102. C. vagum
103. C. vinaceum
104. C. fuscostratum
105. C. atrovirens
106. C. caeruleum
107. C. paniculatum

A few words of explanation are needed in regard to the presence in the list of No. 34, *Coniophora corrugis*, a species which occurs on conifers at high altitudes of the Rocky Mts. and further westward from Washington to Arizona. The gatherings of *Coniophora corrugis* usually have white spores; only one of the 15 gatherings of this species received during a period of 14 years had the spores fully mature and colored.

Inspection of the Key to the Species shows how completely all tissues of the fructification have been used in dividing and subdividing the 4 primary groups.

The form and size of spores, details of paraphyses, gloeocystidia, and chlamydo-spores, arrangement of component hyphae and their histological details and whether stratose or not stratose, and the thickness of the fructification—all are used. For example, in minor group 1 of main group I., consisting of 23 species, after *Corticium paraphysatum* and *Corticium sulphureum* are set apart from the others by highly conspicuous characters, the remaining 21 species are arranged in small sections according to whether their spores are globose or elongated. In the globose-spored section of 7 species, *Corticium punctulatum* and *C. vellereum* are noteworthy by having imbedded chlamydospores which are conspicuous in the sectional preparations. There remain only 5 other species of this globose-spored section to be compared in detail with the characters of a specimen in course of identification which belongs here. In the case of the companion elon-gated-spored section, subdivision of its 14 species on the basis of size of spores and presence or absence of hyphal incrustation results in subsections of 3, 5, and 9 species respectively.

The importance of tissues of the fructification in the work is well shown by the description of *Corticium galactinum*, one of the 9 species of the above group. *C. galactinum* is one of our common species, saprophytic on rotting logs of fron-dose and coniferous species, on the ground, and sometimes parasitic on living roots of the blackberry and apple. The description is as follows:

Fructifications long and broadly effused, becoming rather thick, coriaceous-soft, closely adnate, small pieces separable, white to cream-color, waxy, even, not cracked, the margin indeterminate, thinning out, with the hyphae interwoven; in section 200–1000μ thick, not colored, composed of suberect, densely inter-woven, hyaline hyphae about 1–2μ in diameter, not incrusted; no gloeocystidia; curved ends of the hyphae or their branches form the surface of the hymenium and are about 1/2–1μ in diameter; spores white in spore collection, 4–5 1/2 × 2–3μ.

The few lines of the above description which give the structure of the fructi-fication in section and the characters of its component hyphae are very important and should never be disregarded by anyone following my work.

Turning now to primary group II. of the Key, we find 56 species listed under some character of the tissues so distinctive that it should lead to the recognition of any one of these species. These comprise more than half the North American species of *Corticium*. It was certainly a surprising conclusion to my work to show that more than half the species with us of this difficult genus have histological structure available for their ready specific recognition.

Of the tissues affording distinctive characters, gloeocystidia occur in 31 species so well developed as to be easily visible with the microscope in prepara-tions stained with eosin. It seems quite probable that gloeocystidia are present also in less fully differentiated form in other species which I have left in primary groups I. and III. An example is *Corticium ochraceum*, No. 51 of the list. I believe that I have detected gloeocystidia in stained sections of this species while the sections were still in aqueous mounts. These presumable gloeocystidia are of the same form and dimensions as the neighboring hyphae, from which they are not distinguishable after addition of glycerine to make the mount permanent.

In what may be regarded as their simplest, little differentiated form, gloeocystidia are hyaline, elongated bodies, as in *Corticium lactescens*, No. 63 of the list. In more differentiated form they become pyriform or globose although still hyaline, as in *Corticium polygonium*, No. 78 of the list. A less frequent modification is the differentiation of a permanent color, as in *Corticium debile*, No. 83 of the list, with the gloeocystidia elongated. In further modification they are colored, subangular or globose and sometimes of resinous appearance, as figured by v. Höhnel and Litschauer for *Peniophora serialis*.

Paraphyses. In addition to the production of basidia as terminal branches of tissues of the fructification, other branches which are sterile occur between the basidia. These sterile branches have the general name paraphyses. The paraphyses are often not distinguishable from immature basidia; however, in 18 of our species of *Corticium* the paraphyses have become so conspicuous that they afford a useful specific character. In a few instances these organs are not confined to the hymenium but occur throughout the whole thickness of the fructification, as in *Corticium investiens*.

There is interesting variety in the form of the paraphyses. Sometimes they are very slender, unbranched hyphae which are conspicuous by their abundance and by protruding in the hymenium beyond the basidia, as *Corticium galactinum* and *C. ravum*; sometimes they have 1, 2, or 3 short lateral branches near their tips, as in *C. Atkinsonii* and *C. pilosum*. In other species the branches may be more numerous and somewhat racemosely or paniculately arranged, as in *C. roseum* and *C. paniculatum*. Or the branching may have antler-shaped form, as in *C. investiens*.

Where conspicuous the above characters are very helpful as specific characters but I do not concur in the usage of some mycologists to regard such characters or the gloeocystidia as of generic weight. When regarded as generic, all the convenience of referring to such characters when merely conspicuous is more than offset by the difficulty of locating such characters in all the other species where they are inconspicious and, by the errors in taxonomic work which result when they are overlooked.

In 6 species, chlamydospores are produced normally and conspicuously in the interior of the fructifications. Another species has green basidiospores. Such noteworthy characters set out their respective species sharply.

This study has been based upon so large a body of species that it seems probable that the Corticiums of the world might be classified with advantage in the same way.

KLEBS' THEORY OF THE CONTROL OF DEVELOP-
MENTAL PROCESSES IN ORGANISMS, AND
ITS APPLICATION TO FUNGI[1]

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Thirty years have passed since the appearance of "Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen" by Professor George Klebs ('96). His earlier work and papers all led up to this significant set of researches, and other papers followed in quick succession, all imbued with a straight-forward and simple philosophy concerning the nature and potentialities of organisms.

To understand Klebs and his viewpoint, it is necessary to study all his writings and to take into account the larger outlook and more mature expressions concerning the nature of plants, which in his later papers had become more definitely crystallized.

His work did not attempt to deal directly by experiment with the ultimate structure of organisms, with reference to how plants have become what they are. This is clearly shown in a later paper ('13), in which he states distinctly that living cells, according to his view, are only influenced during their life-time, in three ways; (1) the specific structure; (2) the internal conditions; and (3) the external conditions.

The first of these, namely, "the specific structure" was understood by him to be concerned with what is recognized elsewhere by biologists as having to do with heredity. The other two he clearly believed to come entirely within the scope of the term *environment*, internal as well as external.

According to him, "the specific structure embraces the sum of all the potentialities which are given by molecular structures of the real cell-substances in their physical arrangement"; these he says, "are unknown to us."

Klebs, like any other biologist, must have known at this time of the importance of the newly discovered Mendelian laws, and of some of the earlier discoveries in heredity stimulated by Mendel, and I have no doubt that he accepted them in so far as they seemed to him to be derived from experiment. The essential point to be kept in mind is that these new facts did not appear to him to solve the intricate problem of *how* the "specific structure" really acts to produce these genetic phenomena, nor did they seem to explain the fundamental questions of how development proceeds. The problem as to what values are to be assigned to the internal and external relations of the organism, once

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it was supplied with its quota of hereditary characters (or, as he puts it, "the sum of all the potentialities"), still remained as complex as before.

The study of environment today has two meanings, and these are not always kept distinct by those who refer to environmental researches. The first of these involves investigation into the mechanism of heredity associated with sexual reproduction, where the effect of environment on the germplasm is the object of the inquiry. The second has to do with those studies concerned distinctly with morphogenesis, or the development of an organ after the initial of the organism to which it belongs has come into existence. The latter deals with distinctly different problems than does the former. In the latter case, the fertilized egg or any other single cell that is capable of developing into a mature organism, already possesses all those potentialities which it will ever possess. To the sum of these potentialities it is supposed that neither additions nor subtractions can be made by the environment in the sense in which it is here used. Any of these potentialities may remain abortive, to be sure, due to environmental influences. This, I believe, was also the conception in the mind of Klebs. Once, however, the cell with all the potentialities which are peculiar to the species or other separate unit to which it belongs, has been launched on its career of development, then it is, and not till then, that the matters that will concern us mostly in this paper, are of consequence.

The phrase "external environment" is used rather consistently by botanists and needs no comment here; with reference to the "internal environment," although doubtless there is a vague notion among physiologists that they are referring to it under the term "correlation," I doubt whether the full consequences of its activities are considered in present day experimental work.

Klebs has made clear, over and over again, that the internal environment is an exceedingly complicated complex of influences and that each cell of a metaphyte reacts and is acted upon by its neighboring cells as well as by many of the tissue-cells far removed from such a cell, that, in turn, the external environment, physical or chemical, which acts on the plant as a whole, or on any of these cells or tissues far removed from the cell in question, may transmit its effects through these distant parts on the part under observation. This implies a complexity of physiological reactions and problems not to be lightly approached by the experimental physiologist.

Two considerations are involved in the type of experimentation necessary when one studies his organisms in the light of these conceptions of Klebs. In the first place the definition of "the specific structure" implies its *constancy*. In the second place, by virtue of such constancy, to use the words of Klebs ('13), the organism has "the ability to give like reactions under the same conditions," "while a different species under the same conditions would show other reactions." He clearly recognized that, on occasion, this constancy may be interfered with for some unknown reason, and that in such a case a *mutation* may result.

But even today, with the constant accumulation of evidence that *mutation* is going on in plants generally, and that temporary somatic changes in certain characteristics of a plant, especially in the thallophytes, may occur, nevertheless

this constancy is such a marked feature in so many species and even "forms" of plants, and is so highly and extensively developed, that the assumption of its general presence and dependability is not to be lightly gainsaid.

Whatever tendencies have been showing in the botanical sciences from time to time, to cast aside the historic structure of taxonomy, to belittle the efforts of those botanists who have organized or are reorganizing the plant kingdom by characters that persist and can therefore be recognized by succeeding generations of men,—such attitudes on the part of some botanists have only succeeded in producing loose and indefinite accounts of work done under such influence, and have brought about—what is evident at this very moment,—a greater sense of the importance and need of systematic botany. Whether we continue to call these taxonomic units species, or whether some other name is used, is here only of passing interest. The matter of fundamental importance to the physiologist and by that fact equally so to the geneticist and systematist, is that there is such a constancy apparent in the successive generations of what we call the same organismal unit, and this constancy has been a marvel to biologists and all thinking persons through the ages. The correlated marvel, that evolution has been going on in spite of, and if we knew its cause, perhaps because of, this relatively persistent constancy, need not at this time concern us.

The so-called "somatic mutations" or "saltations" are being more and more observed, especially in the fungi. Recently Leonian ('25) has brought forward experimental data which tend to show that these somatic changes are merely expressions of fluctuating variability, of a special kind, to be sure, but apparently brought about and reversed through the influence, it may be, of the internal environment. What the nature of these influences may be, which cause a temporary "constancy," we do not yet understand. Even where apparently constant forms of fungi have been isolated, as for example in the water molds, one can not be too sure that a stable species is at hand, without extensive studies of its fluctuating possibilities. In such a case as was reported by Pieters ('15), on the behavior of *Saprolegnia monoica* var. *vexans*, we may well be dealing with a temporary form subject to reversal under proper treatment. Through how many different conditions or through what manipulation such an apparently constant strain should be taken in order to establish its constancy is certainly a vexing question. Furthermore, the human element, the physchology of the experimenter, his temperament and his established viewpoint, are no slight factors in the interpretations drawn from such experiments. It may be well to emphasize here, that without previous taxonomic training of a real sort, a physiologist is in grave danger of being misled in his interpretations of work along this line.

In drawing inferences, then, on the basis of constancy such as we believe does exist in plants, whether this is done from the standpoint of the physiologist or the systematist, it is at once apparent that full account must be taken of the fluctuating variability of organisms within a broad scope of environmental influences.

The experiments of Klebs and his students, as well as those done in my own laboratory, have convinced me that for all essential purposes in the search after

the hidden potentialities of any particular plant, it can safely be assumed that the dictum of Klebs holds, namely, that under the same and identical conditions, barring a genetic disturbance, a specific plant will give like reactions under the same conditions, and conversely, that a different plant—be it called species, variety, form, or strain—gives a different reaction.

When interpretations based on this principle seem to fail, it should be remembered that we are using coarse methods of observation and experimentation, that compared to the delicacy of operation of protoplasmic reactions, our senses, even with the aid of modern appliances, are very inadequate to register all the differences or likenesses in reactions. Furthermore, what may appear as inconstant results when obtained through one type of experimental attack, may become quite obvious when another channel of approach is used.

If we apply the principle of constancy under like conditions, it follows, as I have pointed out elsewhere ('08), that closely related plants, as for example the species of a particular family, may be examined comparatively with reference to their physiological behavior. Like conditions imply a *standard* set of conditions. For each family, or even a larger group, such a standard may, by judicial preliminary experimentation, be devised. Such a set of conditions must combine a series of stimuli that act in a highly favorable manner to produce that morphogenetic reaction which may be desired.

One must not conceive such a group of highly favorable conditions as the resultant of the optima of all the physical and chemical factors involved. For, of all the factors present in any complex of environment some may be favorable for our purpose, while some may act in the opposite manner, so as to offset the effect of the favorable factors. The latter are said to "inhibit" the developmental process and must be eliminated or reduced to inactivity. Thus, either intense light or insufficient light may have an inhibitive effect. A certain chemical, harmful at some concentrations, may be increased or reduced to a concentration in which it may still play a favorable role in nutrition, without taking part in the stimulation required for initiating an organ. Klebs ('96) clearly pointed out the importance of this consideration. The principle of "limiting factors" must not be superimposed on this conception, since its application is in quite another direction.

The correlated principle of Klebs that under the same conditions different species will give different reactions, implies what may be called *physiological specificity.*

This idea of specificity seems to have been much neglected by those who have mistrusted the principles of Klebs. It means, of course, that no two species of *Saprolognia*, or two species of *Oedogonium* will respond alike to the same set of conditions. It means that the expectation of confirming Kleb's or anyone else's results for one species must not be assumed in detail in another species of the genus. Klebs says, speaking of Algae ('95); "in buntem Wechsel schwankt das Verhältnis der Zoosporenbildung zur Aussenwelt, je nach den einzelnen Arten." I have repeated the extensive experiments of Klebs on *Saprolegnia mixta* deBary ('08), on *Oedogonium capillare* Kütz., and with the aid of students on species of

Spirogyra corresponding to the species he used, and have obtained definite confirmatory results when using the same conditions *and the same species*. I have, in all these cases treated with meticulous care certain other species of these genera with the environment used above, but without the same active results. On the other hand, the expected reactions did take place when appropriate other sets of conditions were used on the latter species. In groups of fungi other than the water molds, the same situation prevailed in studies made in my laboratory. It seems to me we can not deny that such specificity exists in plants. Furthermore, it is certain that the sensitiveness to small differences in the environment is often exceedingly great as between two related forms among fungi or among algae. How such specificity is to be made manifest in a non-studied species is merely a routine problem for the experimenter.

In what ultimate structure these potentialities lie, is a very different problem. To the geneticist, whose mind functions in terms of genetical factors and genes, it is all explicable on the basis of the magnificent structure which he has built up on theory and experiment with the germ-cell mechanism. To Klebs, whose mind was concentrated on the flux and flow of an infinitely complex substance, namely, the protoplasm as such, the term "specific substance" held all that was necessary for his purpose. In spite of the great practical value with which the results of breeding have enriched our science, the cytologist is still unable to assure us that the minute structures assumed by the geneticist are the alpha and omega of all that is to be said on the subject.

With this brief and very inadequate analysis of the Klebsian viewpoint, we must here be content. It goes without saying that, in view of the remarkable advances in genetics and cytology during the last two decades, acceptance of his theoretical teachings may have to be modified. But to my mind, such modifications will be largely matters of terminology.

We will turn now to a consideration of certain applications of this viewpoint as applied to the study of development, especially that of the asexual and sexual reproductive organs in fungi. During the last fifteen years problems involving the application of these principles have been investigated by myself and my students. Generally speaking, we have been concerned with two types of problems.

First, a detailed study of individual organisms, with reference to the conditions governing the whole morphogenetic development of such an organism. In these cases, the results were confirmatory of Klebs' results and the outcome merely helped to strengthen more completely our belief in the soundness of his principles. Such were the papers by Kauffman ('08) ('21), by Miss Wuist ('13), by Pieters ('15), by Coons ('16), by Bonar ('24) and by Miss Kanouse ('15).

An analysis of the methods and results presented in these papers shows that morphogenic reactions are controlable, that the definite chemical and physiological combinations of environment are essentially precise for each of the main physiological phases of an organism's development; hence the vegetative, the asexual and the sexual phases come to expression, albeit in the same organism, under different and often contrasting sets of stimuli, and that if one has suf-

ficiently explored the physiological nature of a fungus or other plant, in this manner, such an organism is as subject to our manipulation as is a chemical in a test tube. That an occasional exception appears, due to a genetical disturbance, whose cause is admittedly unknown, does not, it seems to me disturb the physiological value of these results, but from the very fact of their wide application raises the presumption that even genetical disturbances may find an explanation in this tremendous correlation which an organism has with its parts, and its parts with the universe in which it lives.

The second type of problems with which we have concerned ourselves has to do with the practical application of these principles to mycology and phytopathology. They are a logical outcome of the recognition that such principles are fairly established. The questions arose whether comparative studies of groups of fungi by such methods would elucidate and simplify their taxonomic and morphological relationships; whether related fungi would show certain general reactions, especially in the formation of the reproductive organs, in a manner to indicate taxonomic value, and at the same time bring out their specificity; and whether or not sufficiently well-constructed sets of conditions could be devised to obtain at will the reproductive organs throughout such groups and thus facilitate the identification of units of each group.

It has long been evident that two considerations are involved in connection with sexual reproduction in fungi, when they are subjected to such studies. Heterothallism must always be considered in cases of negative reactions in cultures set up for the purpose of getting at a generalization. But heterothallism, interesting and provocative of theory as it is to the cytologist or geneticist, is no longer a marvel in mycology; it is, on the other hand, a distinct source of irritation to the laboratory experimenter who has enough to do without going afield to "India's coral strand" (Blakeslee '20) or Greenland's icy mountains in search of the missing plus or minus strain.

But it is fortunate that evidence is accumulating which seems to show that in many groups of fungi heterothallism is not the prevailing condition, even though such seems to be the case in the Mucorales. But even in these molds, it was possible, as demonstrated by Povah ('17) to apply the principle that under the same approximate conditions, each species of *Mucor* could be cultured and recognized in numerous generations even though only heterothallic forms were used. Here, insofar as the vegetative and asexual phases of the life histories were concerned, the specificity was sufficiently expressed in morphologically recognizable characters, so that we have had no difficulty in later years in recognizing these species when brought into the laboratory. The unfortunate situation in connection with the recognition of species of *Mucor* is the continued disregard by those who report species of the genus of the fundamental necessity of a universal "standard" set of conditions, to which the accumulating species are referred and under which they may be intelligently studied by others. The magnificent work of Blakeslee and others on sexual and other characteristics of the Mucorales has not met the practical need of hundreds of laboratory workers in this respect.

The recognition of the value of such a standard led Leonian ('24) to work out a set of conditions for the Sphaeropsidales in which the culture medium plays a part. We have sufficiently tested this medium of Leonian to believe that it exercises the highest favorable set of stimulations for the production of pycnidia that has been devised. Needless to say, the specificity of the species tried out is distinct for all practical purposes. Speaking only of published accounts, twenty-seven genera and forty-five species have uniformly produced pycnidia on this agar (Leonian '24) (Archer '26). In many of these cases, ordinary laboratory media gave no results. It is only rarely that one species out of any twenty-five, fails to respond.

The importance of a ready and quick means of obtaining pycnidia, especially of parasitic fungi of which the identity is desired, is obvious. One may well ask whether it is of more advantage to plant pathology to keep on with hit and miss mixtures of chemicals and media or whether a general use by all workers of a known, successful medium would not more quickly bring uniformity and stability into our taxonomic system, and have its proper effect in eliminating synonyms and new species (Archer '26).

In the Mucorales all species tested under our standard conditions developed their asexual stage in a uniform manner. In contrast to this, the Sphaeropsidales show exceptions to the rule, although the exceptions are remarkably few. As shown by Coons ('16) and Leonian ('24) light is a formative factor for pycnidial formation generally; so of course it is a favorable factor. Species occur, however, which on agar produce pycnidia equally well in light and dark. A few cases are known to us where they form only in the dark. Such cases represent a high degree of specificity and raise interesting problems.

Wehmeyer ('24) has analyzed the difficulties still to be overcome in finding a general artificial standard medium and conditions for the production of the ascus stage in the stromatic pyrenomycetes. Nevertheless, there seems to be no necessity to make any a priori assumptions that such standard media may not be developed in due time.

In spite of the considerable work done on the Saprolegniaceae (Coker '23), no general standard group of conditions is followed in the comparative taxonomic and life-history studies that have been made on this group. This is in part due to the marked specificity of species, members of groups, or as between genera of these water molds. The physiological behavior of any one species that has not been tested out can not be predicted with certainty, if it falls into certain divisions of the family. And yet there are smaller groups of species in which our knowledge is sufficiently complete so that we can predict what a newcomer of such an alliance will do. For example, the so-called "ferax group" of the genus *Saprolegnia* consists not only of clear-cut species, but also of numerous related or intermediate forms or physiological strains; the latter may, of course, belong to the category of temporary saltations referred to earlier in this paper.

However, all of this group show a remarkable uniformity in physiological reactions, which follow closely the classic results obtained by Klebs ('99) for one of the members, namely, *Saprolegnia mixta*. On the other hand, even when the

morphological characters are but slightly differentiated between two forms of this section, their physiological specificity remains a marked feature.

In spite of the greater physiological differences between any genera or smaller groups of Saprolegniaceae, this whole group, barring heterothallism, has nevertheless a tendency toward a general reaction under an appropriate, standard set of conditions. In the case of *Phytophthora* the physiological reactions of the species of that genus seem to be almost as uniform as in the Mucorales. Each such group, as for example, *Saprolegnia, Phytophthora, Mucor*, however, has its own physiological reactions, and this makes it necessary to develop a standard set of conditions for each taxonomic group. The laboratory worker who can grasp the full significance of these facts, will no longer hunt for a medium,—the perfect medium—which shall be the panacea for all his failures to obtain the morphogenetic result he is after.

Brief reference may be made finally to the use of these principles in the case of the fungous parasites which are normally obligative. In such cases, the experimental attack must be largely focused on the host plant. This situation affords an excellent example of one method that may be used by the experimenter to study some of the reactions connected with adjustments that occur in the internal environment. With the permission of one of my students, Mr. C. W. Waters, I shall very briefly report certain experiments made by him with the rusts, the results of which are not yet published. The object of the inquiry was to determine the conditions that control teliospore and urediniospore formation in a selected number of the Uredinales. The results, with ten rusts[2] show that the formation of the urediniospores can be inhibited and that of the teliospores brought about under proper control of such specific environmental factors as affect the nutrition of the host. This varies with the structure and the physiology of each host. All agencies that affect the specific photosynthetic and metabolic processes of each host produce their secondary reactive effects on the rust and on the type of spore it will produce. Lack of space forbids details. This much can be said, that the successful control with every rust tried has convinced us of the highly efficient nature of the principles applied.

In closing this somewhat didactic and incomplete account of our activities in the field of plant physiology, I hope my colleagues will appreciate that I am not attempting to account for all of the countless phenomena that still press on us for solution, even in such a narrow field as mycology. Nor do I wish to set apart this type of inquiry into the physiology of organisms as of all-embracing importance. For certain objectives, however, in the elucidation of phenomena in connection with developmental processes, the principles of Klebs, and such methods and variations of them as were best suited to each problem, have yielded in our hands a considerable harvest of significant results.

[2] *Puccinia Antirrhini* D. & H., *P. Asparagi* Dc., *P. sorghi* Schw., *P. suaveolens* Rostr., *P. Taraxaci* Plow., *P. triticina, P. sp., Uromyces appendiculatus* Fr., *U. Polygoni* Fuckel, *U. Trifolii* Lév.

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PYRENOMYZETENSTUDIEN III SECTIO
WILLKOMMIOTES GENERIS NECTRIAE[1]

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Die im dritten diesjährigen Hefte der "Angewandten Botanik" vorliegenden Vergleichsstudien an etwa 100 Hypocreaceen enthalten Abbildungen von 51 dieser Pilze, deren Entwicklungsgang meist durch Reinkulturen mit dem Naturmaterial verglichen werden konnte. Die Bestimmung dieser Organismen begegnet noch heute Schwierigkeiten, und manche Lücke in früheren Beschreibungen muss ausgefüllt werden. Originalexsikkate fehlen in vielen Fällen. Dennoch musste eine Entscheidung getroffen werden. Lassen wir sie gelten, so haben wir eine einigermassen feste Grundlage für weitere Forschungen, indem wir diese Pilze leichter wiedererkennen können als bisher. Die Diagnosen sind möglichst ergänzt worden.

Die Reinkultur erwies sich bei den meisten dieser Pilze als wertvolles Hilfsmittel bei dem Vergleiche der Merkmale. Im allgemeinen liess sich eine gute Uebereinstimmung in Bau und in der Grösse der Pilze und ihrer Entwicklungsformen in Natur und Reinkultur feststellen. Die absoluten Schwankungen der Sporengrösse erwiesen sich als sehr hoch bei *Nectria galligena* und ähnlichen Arten (vergl. die nachfolgenden Frequenzkurven). Um so wertvoller zeigte sich die Durchschnittsgrösse, die aus mehreren Hundert Messungen berechnet wurde. Vergleichen wir die Durchschnittszahlen nach Reinkulturen ein und desselben Pilzes auf verschiedenen Substraten, so ergibt sich eine gewisse Abweichung, die als Durchschnittsschwankung bezeichnet worden ist. Aber diese Schwankung ist nicht erheblich, wenn Quellungs- und Keimungsstadien vermieden und möglichst die eben ausgestossenen Sporen gemessen werden. Das nachfolgende Beispiel möge zur Erläuterung dieser Verhältnisse dienen.

Man sieht aus den vorliegenden Messbelegen, dass dieselben Hundertmittel-Schwankungen der Sporengrösse, welche in der Natur auftreten, in der Reinkultur bei ein und demselben Pilze wiederkehren. Daher ist man berechtigt, sowohl Pilzstämme mit 9.2 micron als auch solche mit 12.2 micron Durchschnittslänge als *Nectria coccinea* zu bestimmen, wenn sie im übrigen gut übereinstimmen. Ohne die aus Reinkulturen gewonnenen Erfahrungen würde eine Entscheidung schwer zu treffen sein. Tatsächlich ist dieser Pilz früher häufig als *N. episphaeria* oder *N. sanguinea* angesehen worden. In Zukunft wird man bei Exsikkaten, die ausser der Schlauchform noch typische Konidien aufweisen, in

TAFEL 1. VERGLEICHENDE SPORENMESSUNGEN BEI *NECTRIA COCCINEA* (PERS.) FR.

Herkunft		Askosporengrössen			
		Natursporen, Durchschnitts- grösse	Reinkultursporen		
			Durchschnittsgrösse		Absolute Schwankung Messungen, μ
			Substrat	Messungen, μ	
Fagus,	Bonn	9.2×4.4			
"	Tharandt	10.6×4.3	Gerste	12.7×5.2	10−16×4.5−6
			" (trocken)	10.9×4.6	9−14×4 −5
"	Berlin	11 ×4.4			
"	Cleve	12.2×4.4	Buche	9.3×4.2	8−13×4 −5
			Kartoffel	10.0×4.6	8−12×4 −5
			Lupine	10.3×4.5	8−12×3.5−5.5
			Buche	10.8×4.4	8−14×3.5−5
			Apfel	11.2×4.8	9−13×4.5−5
			Robinia	11.3×4.7	9−15×4 −6

Natursporenmittel: 10.8×4.4 (Schwankung 9.2−12.2×4.3−4.4)
Reinkultursporenmittel: 10.8×4.6 ("   9.3−12.7×4.2−5.2)
Absolute Schwankung in Natur und Reinkultur: 8 −16 ×3.5−6

der Bestimmung dieser *Nectria* ziemlich sicher gehen und sogar, wenn frisches Material vorliegt, unter solchen Umständen auf die Reinkultur ganz verzichten können. Es ist also nicht richtig, wenn man, wie das häufig geschieht, die aus Reinkulturen gewonnen Erfahrung verwirft, weil sie angeblich die Bestimmung erschwert. Im Gegenteil schafft sie nur klare Verhältnisse und erleichtert die Übersicht wesentlich, nachdem die Diagnosen mit ihrer Hilfe ergänzt worden sind. Will man sich eine Übersicht von der mittleren Schwankung der normalen Sporengrösse verschaffen, so kann man sich der Sporenlängen-Frequenzkurven bedienen, die in einigen Beispielen hier zur Darstellung gebracht sind.
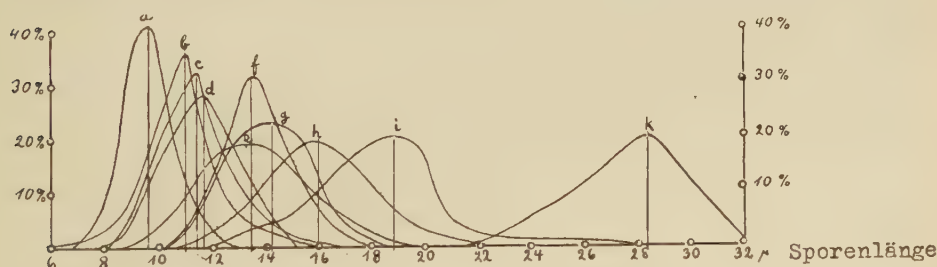
Fig. 1. Sporenlängen-Frequenzkurven bei einigen Nectrien.

Aus der Gestalt der Kurven *e, g, h* und *i*, die einen mehr rundbogigen Scheitel haben, kann man auf eine gewisse Ähnlichkeit dieser Nectrien schliessen. Ebenso ähneln sich die Kurven *b, c, d* und *f* in ihrem steileren Verlauf und spitzeren Scheitel. Beweise für die Annahme einer nahen Verwandtschaft lassen sich

TAFEL 2. SPORENLÄNGEN-FREQUENZKURVEN BEI EINIGEN NECTRIEN.

Nectria-Art	Askosporen					Herkunft
	Durchschnitts-grösse, μ	Quotient Länge Dicke	Epispor glatt, rauh gestreift			
a. peziza	10.3×4.8	2.2	—	—	+	Fagus—Holz
b. sanguinea	11.3×4.0	2.8	—	+	—	Laburnum—Rinde
c. coccinea	11.4×4.5	2.5	+	—	—	Fagus—Rinde
d. " var. sanguinella	11.5×4.4	2.6	+	—	—	Populus—Krebs
e. ditissima	14.4×6.1	2.4	+	—	—	Fagus—Krebs
f. cucurbitula	13.8×4.6	3.0	—	+	—	Picea—Rinde
g. punicea	14.4×4.6	3.1	(+)	(—)	—	Rhamnus—Rinde
h. galligena	16.9×6.6	2.6	+	—	—	Pirus—Krebs
i. ditissima var. major	18.6×6.5	2.9	+	—	—	Alnus—Krebs
k. Jungneri	28.0×9.0	3.1	—	—	+	Theobroma—Rinde

jedoch damit nicht erbringen, denn auch *Nectria peziza*, die einem ganz anderen Entwicklungskreise angehört, hat eine ebenso steil verlaufende Frequenzkurve (*a*) der Sporengrösse wie die vorgenannten. Auch weicht die Durchschnitts-grösse der Spore nur wenig von der der benachbarten Arten ab. Allerdings sind die Sporen deutlich längsgestreift. Der Hauptunterschied der *N. peziza* gegen-über Nectrien mit keulenförmigen Konidien liegt aber in dem Vorhandensein nur einzelliger Mikrokonidien.

Im weiteren Verlaufe der Untersuchungen erwiesen sich als wichtige Merk-male der Bestimmung der Nectrien und nahestehender Gattungen solche der Schlauchform (Gestalt, Grösse, Radialfaserstruktur am Scheitel und Färbung der Perithezien, Vorkommen von Paraphysen, Sporenzahl im Askus, Gestalt, Grösse und Bau der Spore) wie auch solche der Nebenfruchtformen (Konidien und Chlamydosporen). Vergleichen wir nun einmal die im übrigen einander ähnlichen Arten und Varietäten der Gruppe Willkommiotes, so fällt die Tatsache auf, dass manche Arten glatte, andere rauhe oder gestreifte Sporen haben, wieder andere auch Chlamydosporen entwickeln. Die Konidien sind stets von zweierlei Form und Gestalt. Es kommen sowohl kleine meist einzellige soge-nannte Mikrokonidien als auch grössere, zylindrische oder keulige, gerade oder gekrümmte, meist 5–7-septierte Makrokonidien vor, die in tuberkularen Sporo-dochien, als schleimige ausgebreitete Lager oder im Luftmyzel zur Entwicklung kommen und manchmal säulenförmig hervorquellen. Sie sind von weisslicher oder gelblicher Farbe.

Fassen wir die Ergebnisse der Untersuchungen über die bekannten Formen dieser Gruppe in einem Bestimmungsschlüssel, der natürlich die Diagnosen nicht zu ersetzen vermag, zusammen, so können die vorhandenen Merkmale in folgender Weise ausgenutzt werden:

Clavis Analytica

Nectriarum, subgen.   Coryneconnectriae, sect. Willkommiotis, cuius subsectio Leiospora praecipue continet, noxios fungos qui arboribus variis morbum cariem dictum afferunt.
Subgen. Coryneconnectria Wr. (Angewandte Bot. **8**: p. 179. 1926.)

   a. Subsect. Leiospora: Sporidia glabra, ellipsoidea vel ovoidea

          Sporidia 16–19 μ longa

              Conidia 5–7–septata 5–6 μ crassa

                  Sporidia 18–19$\times$6.5–7.2 μ

                      Nectria galligena Bres. var. *major* Wr.

                      (Typus Fraxino cariem affert)

                  Sporidia 15–17$\times$5.7–7.2 μ

                      Nectria galligena Bresadola

                      (Typus Piro aliisque Pomaceis cariem affert)

              Conidia 5–7–septata 4–4.7 μ crassa

                  Sporidia 18.6$\times$6.5 μ

                      Nectria ditissima Tul. var. *major* Wr.

                      (Typus Alno cariem affert)

                  Sporidia 15.2$\times$6.4 μ

                      Nectria ditissima Tul. var. *arctica* Wr.

                      (Typus Betulae pubescenti cariem affert)

          Sporidia 14–16 μ longa

              Sporidia 6.1 μ crassa . . . . *Nectria ditissima* Tulasne

                  (Typus Fago cariem affert)

              Sporidia 4.6 μ crassa . . . . *Nectria punicea* (Schm.) Fr.

                  (Typus habitat in Rhamni cortice)

          Sporidia 10.5–12.5 μ longa

              Sporidia 4.3–5.3 μ crassa

                  Peritheciorum peridium non radiali-fibratum

                      Nectria coccinea (Pers.) Fr.

                      (Typus habitat in Fago)

                  Peridium ostiolum versus radiali-fibratum, conidia 60-70$\times$5.3 μ, ad basim interdum bulbose-tumida

                      Nectria coccinea (Pers.) Fr. var. *sanguinella*

                      (Fr.) Wr. (Typus Populo cariem affert)

                  Peridium ostiolum versus radiali-fibratum, conidia 70–90$\times$6–7 μ, ad basim obtusa

                      Nectria coccinea (Pers.) Fr. var. *tropica* Wr.

                      (Typus ad ramos emortuos Coffeae habitat)

              Sporidia 4–4.3 μ crassa

                Conidia 5(3–7)–septata, sporidia 11.3$\times$4 μ

                      Nectria coccinea (Pers.) Fr. var. *minor* Wr.[2]

                      (Typus ad corticem Laburni habitat)

                Conidia 5–7(3–10)–septata, 82–91$\times$5.6–6 (ad 122$\times$6) μ, sporidia 12.1$\times$4.1 μ

                      Nectria coccinea (Pers.) Fr. var. *longiconia* Wr.[3]

                      (Typus ad corticem Aceris habitat)

   b. Subsect. Trachyspora: Sporidia distincte aspera, plerumque 4.6 μ crassa, perithecia singula vel modice gregaria

                  Nectria cucurbitula (Tode) Fr.

                  (Typus ad corticem Piceae Pinique habitat)

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[2] Wollenweber. Zeitsch. f. Parasitenkunde **1**: 157. 1928.
[3] Wollenweber. Zeitsch. f. Parasitenkunde **1**: 159. 1928.

Nota: Nectriae sectionis Chlamydosporae Coryneconnectriarum differunt a speciebus sub-
       sectionis Trachysporae sectionis Willkommiotis sporidiis plerumque crassioribus, peri-
       theciis majoribus plus minusve mammoideis, chlamydosporis praesentibus.

   c. Subsect. Rhabdiospora: Sporidia plus minusve longitudinaliter striolata
          Sporidia 12.9×7.7 μ
                          Nectria cinereo-papillata P. Henn. et Nym.
          Sporidia 28×9 μ
                          Nectria Jungneri P. Hennings
                          (Typus in Theobroma cacao emortua habitat)

Trotz aller Bemühungen, eine feste Artumgrenzung zu erreichen, bleibt
natürlich eine gewisse Unsicherheit bestehen angesichts der Tatsache, dass
Arten wie *Nectria galligena* Bres. je nach Herkunft und Wirtspflanze verschiedene
Sporengrössen aufweisen, wie folgendes Beispiel zeigt:

TAFEL 3. VERGLEICHENDE SPORENMESSUNGEN BEI *NECTRIA GALLIGENA*. BRES. UND
          N. GALLIGENA VAR. *MAJOR* WR. VERSCHIEDENER HERKUNFT.

Nectria-Isolierung	Sporengrössen		
	Durchschnitts-grösse, μ	Mittlere Schwankung, μ	Absolute Schwankung, μ
Nectria galligena Bres. von			
Pirus malus, Berlin	14.9×6.2	12–17×6–6.5	10–20×5–8
" communis, Berlin	15.1×6.9	12–17×6–6.6	11–19×5–7
" malus, Westfalen	15.3×5.6	14–18×5.6–5.8	12–21×5–6.5
Sorbus aucup., Norwegen	15.4×7.1	13–18×6.9–7.5	10–22×5.5–8.5
Fraxinus exc., Sachsen	15.5×6.1	13–18×5.5–6.5	8–21×5–8
Pirus comm., Norwegen	15.8×6.9	13–18×6.6–7.6	11–20×5–8
" malus, Sch. Lippe	16 ×5.7	14–17×5.7–6.0	12–22×5–6.5
" " Berlin	16.5×5	14–18×5–6	12–23×4–7
" " Sachsen	16.8×6.4	15–18×9.6.6	12–25×5–9
" " Norwegen	16.9×7	14–19×6.5–7	14–22×6–8
Salix, Österreich	17 ×5.8		15–20×5–7
Populus, Norwegen	17 ×7.2	15–19×7–7.5	11–22×5.5–9
Pirus malus, Oregon	17.1×6.9	15–19×6.6–7.4	12–22×5–8
Sorbus aucup, Holland	17.2×6.4	14–19×6–7	12–25×5–8
Nectria galligena Bres. var. major Wr. von		16–18×6.5–7	11–22×6–9
Fraxinus exc. Westfalen	18 ×6.7	17–19×6.8–7.5	13–25×6–9
" " Brandenburg	18.2×7.2	17–21×6–7	14–25×6–8
" " Hessen	18.8×6.7		15–22×6–8
Salix, Sachsen	18.6×6.5		

Der Schwankungsbereich der Sporen-Durchschnittsgrösse bei *N. galligena*
von *Pirus*, 14.9–17.1×5–7μ, stimmt also auch mit dem von *Sorbus*, *Populus*,
gelegentlich auch einmal mit einem von *Fraxinus*- und *Salix*-Krebs festgestellten
überein.   Die meisten *Fraxinus*-Krebs-Nectrien haben jedoch Durchschnitts-
grössen von 18–19×6.5–7.2μ, wie sie sich auch bei *Salix* finden.   Im Vergleich

zu *N. galligena* hat die Buchenkrebs *N. ditissima* kleinere Sporen, 14.4×6.1μ, und schmalere, längere Konidien, die Erlenkrebs *N. ditissima* var. *major* dagegen grössere Sporen, 18.6×6.5μ, und höher septierte Konidien. Diese Nectrien haben glatte Sporen (subsectio Leiospora), während *N. cucurbitula* etwas rauhsporing ist.

SCHLUSSBEMERKUNG

Wenn wir auch die Tatsache anerkennen müssen, dass die Nectrien der Gruppe Willkommiotes einander sehr ähneln, so sind doch die vorhandenen morphologischen Unterscheidungsmerkmale konstant genug, um ihre Auseinanderhaltung zu rechtfertigen. Auch müssen wir berücksichtigen, dass einige Arten pathogen sind, andere nicht. Zu den letzteren gehören, wie es scheint, *N. punicea*, *N. coccinea* und *N. Jungneri*, wenn es auch nicht ausgeschlossen ist, dass einige gelegentlich Rindenfäule wie *N. cucurbitula* (an Coniferen) hervorrufen. Keine der genannten Arten ist mit Krebs vergesellschaftet gefunden. Im Gegensatz dazu stehen die krebserregenden Nectrien wie *N. galligena* (Pirus-Krebs), *N. galligena* var. *major* (Fraxinus-Krebs), *N. ditissima* (Fagus-Krebs), *N. ditissima* var. *major* (Alnus-Krebs), *N. ditissima* var. *arctica* (Betula-Krebs) und *N. coccinea* var. *sanguinella* (Populus-Krebs). Infektionsversuche sind auf breiterer Grundlage von H. Richter[4] in Dahlem durchgeführt worden, die die Frage klärten, wie weit sich die genannten Arten vertreten können bzw. wie weit ihre Spezialisierung vorgeschritten ist und wie weit das Vorhandensein von Nectria-Krebs an einer Wirtspflanze eine Gefahr für die in der Umgebung befindlichen Nutzpflanzen bedeutet. Für eine wirksame Bekämpfung können diese Kenntnisse nicht entbehrt werden.

SUMMARY

1. In pure culture as well as in nature the Nectrias of the section Willkommiotes and related fungi studied develop spore forms with a similar absolute and average fluctuation in size.

2. As a result of these comparative studies the borderline of some species such as *Nectria coccinea* could be easily fixed.

3. The borderline of other species such as *Nectria galligena* has been restricted to strains averaging from 14.9−17.2×5−7.2μ in the spore size. These will include most of the apple canker producing Nectrias. The *Fraxinus* canker *Nectria* with spores averaging 18−19×6.5−7.2μ, *Nectria galligena* var. *major*, seems to be absent on *Pirus* but present on *Salix*. *N. galligena* has been found on *Pirus*, *Sorbus* and *Populus*, rarely on *Fraxinus* and exceptionally on *Fagus*. Some of the canker producing Nectrias seem to be more specialized than others.

4. An analytic key has been worked out to facilitate the determination of the 14 Nectrias belonging to the section Willkommiotes of the subgenus Coryneconnectria.

[4] Richter. Zeitsch f. Parasitenkunde 1: 24–75. 1928.

THE PROBLEM OF A NATURAL CLASSIFICATION OF THE ASCOMYCETES[1]

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It is now generally accepted by biologists that the basis of a natural classification of animals and plants is the belief that the origin of species and all other groups has been by a process of evolution and development from earlier forms. There may be disagreement in regard to the methods and causes of evolution, but all scientific taxonomy is supposed to be based upon this concept. If we knew or could trace the ancestry of these fungi we could secure the information necessary to determine the phylogeny of the group and thus solve the problem of a natural system. If the geological record furnished as much information regarding the past history and ancestry of the fungi as it does of the flowering plants we might perhaps get some important clues. Unfortunately, paleontology has thus far thrown very little light on the phylogeny of the fungi. This is probably due to the perishable character of most of the species, which has prevented their preservation in fossil form. We must, therefore, seek in other directions for the information necessary to determine their derivation and relationships.

Thirty years ago I thought the problem rather simple, and that I might soon be able to make important contributions toward a natural system of the fungi, especially of the Ascomycetes. Such is the conceit of youth and ignorance. Now I am wondering whether the human race will survive long enough to solve the problem. Like many problems in biology, if we had an adequate comprehension of its complexity and difficulty we should be disposed to abandon it in despair. On the other hand, with a broad general understanding and thorough analysis of the problem and with much patience and persistent research, it is possible to make valuable contributions to our knowledge of the subject.

As we study and compare the fungi it becomes more and more evident that these organisms were not created for the innocent amusement and recreation of the taxonomic botanist, and that they do not conform to our ideas of natural groups. Thorough studies of their life histories and morphology are demonstrating the extreme difficulty of identifying and determining species and genera, and are showing the great need of much more complete and profound knowledge of these organisms before any worth-while attempt can be made toward a natural classification. Vastly more material is needed for comparison, and more thorough and extensive field studies are required.

[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, Aug. 18, 1926.

In this discussion I do not propose to consider the origin of the Ascomycetes. Much time and effort have been spent on this question already without very satisfactory results. The crying need at present is more accurate knowledge of the morphology, cytology, and life histories of the forms already known and more general and diligent search for the unknown forms, which may supply some of the missing links in the phylogenetic chain.

In determining the natural relationships and taxonomy of the Ascomycetes, as in all other groups, a thorough study must be made of all phases of the subject which may throw any light upon it. As already stated, the paleontological records give us little or no help at present. The other principal lines of investigation which should help solve this problem are geographic distribution, physiological characters, morphology, and cytology of reproductive organs, life histories of the species, and their morphology and development.

We know so little about the geographic distribution of most of the species at present that few conclusions of any value can be drawn from this source. Certain species of the group appear to be somewhat cosmopolitan, though erroneous identifications are so frequent that the report of a certain species in any locality can not be depended upon.

Whether the age and area theory can find any support in the distribution of the Ascomycetes I am not prepared to say. It does appear, however, that some of the forms which we regard as ancient have a very wide distribution in tropical and temperate regions.

Physiological characters are of value chiefly in determining sub-specific relationships. I do not regard it as practicable to use purely physiological characters for specific segregation. Host relations and parasitism have frequently been used by mycologists as the basis for species. This has led to great confusion and to useless multiplication of so-called species. Parasitism is a function which is apparently rather readily acquired by fungi and does not alone furnish a satisfactory basis for the separation of species or higher groups. Parasites and saprophytes frequently occur in the same genus.

The morphology and cytology of the reproductive organs should furnish valuable information in regard to the relationships of these fungi, if we are justified in assuming that these organs have similar taxonomic value here, as in the higher plants. Much further knowledge, however, of the different forms of these organs and more exact information in regard to the nuclear phenomena in a much larger number of cases in different groups must be obtained before these characters can be safely coordinated with other important characters and be utilized in natural classification.

Gwynne-Vaughan has recently attempted an arrangement of the Ascomycetes on the basis of the characters of the sexual apparatus. The result, however, is not satisfactory and leads to the bringing together of forms which according to their morphology and life histories are not closely related. Similarity of these organs, however, in certain Pyrenomycetes and Discomycetes may indicate a relationship not heretofore considered. However, the fact can not be too frequently or too strongly emphasized that any system based upon a single character must result as an unnatural arrangement.

Our increasing knowledge of the fungi as well as of other organisms emphasizes the great complexity and diversity of their characters and relationships. The Ascomycetes present special difficulties because of their pleomorphism and heterothallism. Some are known to have three or more spore forms in their life cycle. The life cycles of comparatively few species have been accurately determined and but little attention has been given to the consideration and determination of their taxonomic value. It has been suggested that the conidial and pycnidial stages, being essentially vegetative forms of reproduction, have no more taxonomic significance than bulbs and tubers have in the flowering plants. We do not think such a conclusion is justified, however. This is primarily a question of fact, which can be determined only by a thorough study and comparison of the various forms which occur.

The conidial and pycnidial fructifications, or deuteroforms, as they may be called collectively, since we have no simple equivalent for the "Nebenfruchten" of the Germans, are much more highly differentiated and complex organs than bulbs and show a much higher degree of development and specialization.

Our present knowledge of the life histories of this group, though scanty, shows something of the great variety of forms which occur, and I presume eventually nearly all the Deuteromycetes will be connected with their ascogenous stages. Of course it is possible, if not probable, that some may have lost their perfect stages and become autonomous. It is a question in such cases whether they were originally simple or whether they have become so by the loss of other forms. Some ascogenous forms also appear to have no lower spore forms. It is extremely difficult to prove, however, that an ascogenous form has no other stage, as there is always a possibility, if not a probability, that the proper conditions have not been provided for its development, or else that it may be heterothallic. The important question is what taxonomic value has these forms. The answer to this, as to other questions of a similar character, depends upon a thorough knowledge of each individual case. No generalization can be made. In some cases, as in *Botryosphaeria* and *Physalospora*, the ascogenous forms are so similar morphologically that they were until recently regarded as a single species. The pycnidial form in the first case is, however, *Dothiorella*, and in the second case *Sphaeropsis*.

We have, after much consideration and argument both *pro* and *con*, decided that this difference in the pycnidial stages is sufficiently great to justify the recognition of the two genera, notwithstanding the fact that one may not be able from a microscopic examination of either perithecial form to determine in all cases with certainty to which genus a particular specimen belongs. The fact that both of these generic names are already in use might be urged as a practical reason for retaining them. We do not expect all mycologists to agree with us in this case, as other considerations might seem to them of greater importance.

A similar condition obtains in other cases. For example, in *Mycosphaerella*, which has been so ably investigated by Klebahn. Here we find perithecial forms very similar, or in some instances almost identical morphologically, which have different "Nebenfruchten." In one case it may be *Ramularia*, in another *Cer-*

cospora, and in another Septoria or Ascochyta. Other deuteroforms also are known. In this case Klebahn has concluded that the groups having dissimilar deuteroforms should be treated as distinct genera, and has proposed the names Ramularisphaerella, Cercosphaerella, and Septorisphaerella for them. These are, of course, suggestive names, but they are long and cumbersome. The primary question however here, as elsewhere, is whether these conidial and pycnidial forms are of sufficient uniformity and constancy to furnish a satisfactory basis for the segregation of genera.

In the case of Ramularia and Cercospora all sorts of intermediate forms seem to occur, so that it is difficult to separate them. The same is also true of Septoria, Ascochyta, and Phleospora, which are also the pycnidial forms of some Mycosphaerellas, while microsporic forms also occur. For this reason we do not think we are justified in concluding that similar ascogenous forms having different deuteroforms should always be treated as distinct genera.

The work of Wollenweber on the life histories of the Hypocreaceae also shows how diverse and varied the conidial conditions may be in a group. In Nectria, for example, the perithecial stages are very similar and the conidia very diverse. Instead of basing genera on the different conidial forms he has followed a plan opposite to that used by Klebahn, maintaining the genus in the broad sense and dividing it into 4 subgenera, 11 sections, and 8 subsections. I fear that this is perhaps erring in the other direction, and that it would better meet the practical as well as scientific purposes of mycologists to recognize more than one genus here. Just how many, however, would not be easy to determine. Each case must be decided upon its merits and determined by the nature and importance of the deuteroforms and their coordination with other characters in the ascogenous forms. If followed blindly, making differences in deuteroforms the basis of segregation of genera, it might lead to confusion and inconvenience rather than service to mycology.

There are other cases among the Ascomycetes in which the opposite condition prevails, that is, in which very dissimilar ascogenous forms have very similar deuteroforms—for example, Glomerella, Gnomonia, Pseudopeziza, Trochila, and Plectodiscella, representing both Pyrenomycetes and Discomycetes, all have Gloeosporium-like conidia.

The question arises here as to whether this is merely parallelism in development of conidial forms or whether it indicates closer relationship between these widely different genera than usually supposed. It should be observed, however, that a careful morphological comparison of the conidial forms in these cases shows certain differences which might perhaps be regarded by some as of generic value, though the acervuli and spores are very similar. This similarity of deuteroforms probably does not indicate near relationship between these Pyrenomycetes and Discomycetes, in view of the great morphological differences between the ascogenous forms. Until we have more knowledge on this subject no definite statement can be made, however, as to the relative value and importance of such characters. Similar cases are known in other groups, for example, Monilia or Monilia-like conidial forms are known to occur in quite different genera of

Ascomycetes. *Stilbum* or *Stilbum*-like forms belong to *Omphalia* among the Agarics and also to Hypocreaceous genera.

Other cases of both kinds might be cited, but these are sufficient to show some of the complexities and difficulties involved and the necessity of a thorough knowledge and consideration of the life history of any ascomycete before anything final can be said regarding its relationships and taxonomic limitations.

Many interesting questions also arise as to the significance of the mere presence or absence of deuteroforms among the Ascomycetes. Are groups having no such forms to be regarded as high or low, ancient or recent? Were they originally simple, or have they become so by loss of other spore forms? Do deuteroforms disappear entirely or do they become autonomous or both? It is difficult to determine these questions. To prove with certainty that a deuteroform is autonomous, it would be necessary first to know the life history of all Ascomycetes. It is well known, of course, that such forms can live for many generations without the interpolation of the ascogenous stage, and on account of the continual failure to get such forms to produce ascocarps under artificial conditions, it has been assumed that they have been lost. This assumption is of little value, however, in view of our lack of knowledge of the necessary conditions for the full development of many species, which readily complete their life cycles when started from ascospores. The life cycle of these species is, however, not completed under the same conditions when deuterospores are used. As to the presence or sequence of development of the different stages in the life cycles, we have not sufficient information to furnish an answer to these questions, and it is quite within the range of possibility that the different modes of origin suggested or even others may have occurred.

Nature is continually surprising us by her great versatility, and to regard her plans and methods as simple, usually means failure to interpret her correctly.

Furthermore, the functions of some of the pycnidial forms is not yet thoroughly understood. Some of those which have been called spermogonia are still regarded as either functional or vestigial male organs. Failure of attempts to germinate the spores or so-called spermatia of such forms were at first regarded by Tulasne and others as evidence that they are not simple asexual reproductive bodies. The failure of germination has in many cases been found due to lack of proper conditions for growth. Cornu was unable to germinate many of the so-called spermatia; others have been germinated since.

After all has been said, morphology must be the chief basis of systematic botany, if it is to be of general application and usefulness. The extreme specialist in pathology may discover physiological differences as to parasitism, host relations, or other functions, but these are of minor taxonomic significance and should be classified as physiologic forms and not species. If it is accepted that morphological characters must be our chief source of information in determining genera and species, it naturally follows that the more perfect our knowledge of such characters and of their relative value and stability the better prepared we shall be to determine the limitations of the different groups and their relation-

ships. It may therefore be desirable to consider the principal morphological characters of ascocarps and their taxonomic value.

In order to be specific let us examine some of the characteristics upon which the present arrangements of the Pyrenomycetes are based. Saccardo's system, being well known, will answer our purpose. The presence or absence and character of the perithecia and stromata form the chief basis of family segregates. The Hypocreaceae are distinguished principally by bright-colored, fleshy, or waxy perithecia and stromata, and the Sphaeriaceae by dark-colored or black perithecia and stromata. It is true that there is a more or less natural group of Pyrenomycetes which generally possesses the characteristics mentioned, but life histories and other characters show that some genera having colored, waxy stromata do not belong to Hypocreaceae—for example, *Endothia* and *Polystigma*. Between the Hypocreaceae and Xylariaceae there are many intermediate forms which connect the two families and render it extremely difficult to make a satisfactory separation. Such genera as *Podosordaria*, *Xylocrea*, *Thuemenella*, and *Peridoxylon* are good examples.

Genera are usually separated, not only by Saccardo but by others, on the basis of differences in ascospores, such as color and septation, and also on the presence or absence of stromata. Spore color is in many cases a most uncertain and unsatisfactory character. The same is true of spore septation. Spores may be expelled in a hyaline condition and germinate and reproduce normally, but others of the same species may become colored later. This is the case in *Massaria plumigera* and also in other genera and species. Then, of course, there are all intermediate conditions found in color in fully mature spores of different species. Some show slight or distinct color in mass, but appear colorless when scattered on a slide.

Spore septation is even more unreliable in many instances. Some spores appear mature but non-septate, but later become one or more septate. Normally three-septate spores may appear mature but have only one septum. In some genera and species, however, both color and septation are remarkably constant. With these as with all other characters constancy and taxonomic value must be determined by observation and experience in each case. In one instance they may be constant and reliable and in the next inconstant and unreliable. The same is true of stromata, of which so much use has been made in the separation of genera and species and even families. A stroma is merely a mass of non-sporogenous fungus hyphae, forming a pseudo-tissue ranging from loose plectenchyma to pseudo-sclerenchyma in or upon which the fruit bodies or sporogenous hyphae are produced.

A stroma may be present or absent in any family of fungi, just as there may be herbs, shrubs, or trees in any family of flowering plants, and has no more taxonomic significance. In some cases stromatic characters are fairly constant for a genus. In other cases they are not reliable for specific segregation. The only characters separating *Rosellinia* from *Hypoxylon* in many cases is the lack of stroma in *Rosellinia*. Different species, however, have been transferred from one of these genera to the other because in one case the author considered the

stroma present where others regarded it as wanting. In fact, one can frequently find specimens of the same species, for example *Hypoxylon crustaceum* and *Rosellinia subiculata*, in which some of the perithecia are united in a thin stroma and others are separate. The conidial forms in both genera are very similar. The subiculum present in such species as *Rosellinia aquila* is simply the equivalent of a stroma, but of a loose, felty character.

In view of these facts it would seem that in any attempt at a natural arrangement of the fungi these two genera should be in the same family instead of in different widely separated families, as is usually the case.

The presence or absence and the character of the ostiole or beak in the Pyrenomycetes are of little taxonomic significance in many cases. We have frequently found, for instance, specimens of the same species of *Eutype* with beaks almost lacking, and all intermediate conditions between these and beaks one-half inch long, depending upon the conditions of shade and moisture under which the plant was grown.

The taxonomic significance of paraphyses is also doubtful in many cases. They apparently may be present or absent in some species but are constant and uniform in character in some other cases.

Gäumann in his recent book on the Comparative Morphology of the Fungi says (translated): The structure and appearance of the perithecia have been used empirically in the arrangement of the Sphaeriales—for example the Hypocreaceae—while their life history, development, internal structure, and deuteroforms have been neglected.

It seems probable that entirely too much importance has been placed upon the form of the fructification in the Ascomycetes, that is, as to perithecia and apothecia. The difference in these two forms of fruit bodies are perhaps more conspicuous than important. Many intermediate conditions and forms are known. The chief difference between the two is the greater development in the Discomycetes of the fertile portion of the ascocarp, that is, the asci and paraphyses.

It seems probable that instead of having two more or less distinct and parallel lines of development in the Pyrenomycetes and Ascomycetes, as is usually supposed, divergent forms have arisen in both lines. Some perithecial forms may have been derived from apothecial forms and *vice versa*. More evidence of this will probably appear as our knowledge of life histories and development increases and as many at present unknown forms are discovered.

In most of the taxonomic mycology of today there is much evidence that we still have the millstone of tradition and authority about our necks. While nominally accepting a new law and order of Nature, that of evolution and diversity, in practice we follow the same old methods and systems.

We must approach these problems from every possible angle and in an unprejudiced and receptive state of mind, continually keeping before us the fact that Nature's ways are not simple and that any system based upon a single character is almost certain to lead astray. There is no knowledge of a plant which can not throw some light upon its relationship, if properly interpreted.

The title of this paper, "The problem of a natural classification," etc., was premeditated, and you have probably already noticed that we have done little more than attempt to present some of the chief points in this problem as we see it. In many cases in undertaking botanical investigations we rush in and attempt to solve a problem before we have any clear conception of its true nature and difficulties. As already remarked, if we did really appreciate the complexity of some of these problems we would either abandon them or proceed with far greater consideration, diligence, and caution.

If there is any truth in these statements, it should be very evident that the solution of the problems of taxonomic mycology is not for the novice nor for those who think the solution simple. In order to make real and permanent progress in determining the phylogeny and relationships of the fungi the work must be based upon a broad general knowledge of biology and upon thorough studies of comparative plant morphology in general, as well as with special reference to the fungi. All the information which cytology and developmental histories, as well as physiology, can furnish in addition to life histories and morphology, should be considered. The thorough study of a genus or group of species from every aspect will throw much light upon the difficulties connected with the nature and limitation of taxonomic groups and their relationships.

It has been asserted that various taxonomic groups, and especially genera and species, are merely intellectual concepts and that they do not exist as distinct entities in Nature. Of course in order to prove absolutely that any group of individuals designated as a species is distinct from all other groups it would be necessary to examine all individuals of the species and compare them with all other closely related species. This is confessedly impossible. We may, however, I believe, secure sufficient evidence to justify a tentative conclusion. I believe there are undoubtedly groups of individuals which show no intergrading forms with other groups. For example, such species as *Pyronema confluens*, *Glonium stellatum*, *Angelina rufescens*, and *Plowrightia morbosa* appear to have so such close relatives as to cause difficulty in identification. Whether these groups coincide with the general idea of a species or not is another question. It seems equally true in certain groups of genera and species that the evolutionary process is now in active operation and that all kinds of intermediate forms are to be found, so that for taxonomic purposes the segregation of species must be more or less arbitrarily made for convenience in cataloging and for other practical purposes, if for no other reason. Such is the condition apparently in the genera *Eutypella*, *Valsa*, *Diaporthe*, and others.

Among the apparently distinct groups of genera and species the evolutionary process might be said to have reached a temporary state of equilibrium, that is, there is no active change going on and the groups and individuals are distinct and temporarily stable.

Nothing approaching exact standards of measurements for the determination of genera and species, however, can be devised. If we should define a species as the smallest group of individuals showing the same morphological characters we should have in some cases such species as the so-called elementary species of

Jordan, and beside these such species as those of Linnaeus. For practical pur-
poses, therefore, it appears necessary to use the term species for groups of in-
dividuals which can be separated by recognizable morphological characters,
admitting that in many cases these groups are somewhat arbitrarily established
and that there are integrading forms with other species.

From the foregoing considerations and remarks it would seem evident that
if a permanent contribution to systematic mycology is to be made, more ability,
knowledge, and experience are required than in most other branches of botany.
Many years of training and experience in the laboratory, herbarium, and field
are essential to the successful undertaking of monographic work in any group.
The same is true in regard to the determination and description of new species.
It is an extremely difficult matter to determine under present conditions of
mycology whether any particular gathering of a fungus has been described or
not. It involves unusual library and herbarium facilities as well as much field
and herbarium experience in studying the various members of the family and
genus to which the plant belongs. In the present state of systematic mycology
one frequently finds a species placed in a genus in which it would be least ex-
pected, according to the true characters of the specimen in hand.

The conclusion I reach from this consideration of the problem is that progress
toward its solution can be made only by attacking it with intelligence and per-
sistence from every possible angle, being satisfied to contribute small items to
the great mass of knowledge which must be accumulated before even a botanical
genius can coordinate it and give us a natural system.

SOME OBSERVATIONS ON THE SPORE DISCHARGE OF THE HIGHER FUNGI[1]

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ABSTRACT

(a) *The drop-discharge mechanism in the Basidiomycetes.* The Hymenomycetes, Uredineae, some Tilletiaceae, for example, *Tilletia Tritici* and *T. laevis*, and the three species of the basidiomycetous yeast-genus *Sporobolomyces* all develop and discharge their basidiospores in an identical manner. In these fungi: (1) every basidiospore is developed asymmetrically on the end of a conical sterigma; (2) the spore-hilum is formed at the apex of the sterigma; (3) a few seconds before a spore is discharged a drop of fluid is excreted at the spore-hilum; and (4) the spore and the drop are shot violently away together to a distance, varying with different species, of about 0.05–1.4 mm. The drop-discharge mechanism here involved has received no adequate explanation. It is possible that the sterigma and its spore together constitute a surface-tension gun of such a nature that the force of discharge resides in the surface tension of the drop of fluid. Since the Hymenomycetes, the Uredineae, *Tilletia*, and *Sporobolomyces* develop and discharge their basidiospores in an identical manner, they probably owe their origin to a common ancestor.

(b) *The discharge of spores in the Discomycetes and the phenomenon of puffing.* The author has studied the hymenium of certain Discomycetes in surface view and in sections taken in a radial-longitudinal direction through the apothecium. Hitherto no one seems to have investigated the Discomycetes in this manner.

In *Sarcoscypha protracta* Fr. the apothecium is more or less deeply conical, the asci have straight axes, and the operculum of each ascus is situated not symmetrically at the end of the ascus, but asymmetrically, so that it looks toward the mouth of the apothecium as a whole. The result of this is that, when an ascus explodes, it shoots away its spores not perpendicularly to the surface of the hymenium, but in a direction more or less parallel to the central axis of the apothecium. Owing to these arrangements the spores of all the asci easily escape into the air above the apothecium so that they can be carried off by the wind.

The author has devised an experiment with a test-tube having a lateral opening near its end, which conclusively proves that when a fruit-body of *Sarcoscypha protracta* puffs, it produces a blast of air. The air is set in motion by the simultaneous impingement upon it of vast numbers of spores and drops of

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ascus-sap. Puffing is a biologically advantageous phenomenon in that the disturbance of the air caused by it aid in the dispersion of the spores.

In most Discomycetes, for example, *Morchella conica*, *Aleuria vesiculosa*, *Galactinia badia*, *Lachnea scutellata* and *Ascobolus immersus*, the asci are heliotropic, that is, their outer ends bend so that they point toward the direction from which the strongest light comes, and the operculum is situated symmetrically at the apex of each ascus. The result of these arrangements is that, when the asci explode, the spores are successfully shot away from the fruit-bodies into the outer air.

VARIATION IN FUNGI AND BACTERIA[1]

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SUMMARY

An introductory survey of the present position is followed by a brief critique of genetic phenomena, concepts and terminology in groups of organisms other than bacteria and fungi. The two latter groups are then considered and a critical analysis is made of the phenomena of variation that have been described. These may be classified from two points of view; firstly, on a basis of morphological and physiological criteria which arranges the data in phenotypic values and, secondly, according to the factors of their appearance and their mode of behavior, which arranges the data in genetic values. Correlations between the two systems of classification are discussed. The types of variation in fungi and bacteria classified on the genetic basis are treated in relation to processes of growth and reproduction in these groups of organisms: aberrant types of genetic phenomena are considered. Fungi and bacteria are compared with other groups of organisms in respect of the types of genetic phenomena exhibited, the interpretation and classification of these types, the genetic concepts which emerge and the terminology adopted. Finally are considered the avenues and directions of genetic research on fungi and bacteria, and the possibilities and limitations of such research.

A. INTRODUCTION

During the last two decades the study of the genetics of micro-organisms has attracted increasing attention. Protozoal researches have been collated and discussed by Jennings (1920, 1923) Jollos (1924), and more recently by Calkins (1926). The algae have received comparatively little notice, but recent contributions have been made by Pascher (1916, 1918), Transeau (1919), Hartmann (1925), Woronichin (1926), and R. Chodat (1926), and the subject has been discussed by Tischler (1922) and Crow (1924).

The interest of mycologists had long been aroused by the researches of Hansen (1898, 1906, 1907) on the yeasts, by Salmon's (1900, 1905) work on *Erysiphe*, by the studies of Eriksson (1894–1898) and Marshall Ward (1901–1905) on the rust fungi, and by the results of Blakeslee (1906) and Namylowski (1906) on *Mucor*. In the study of bacteria the problems of variability had in various guise always occupied a primary place but a great step forward was taken when Barber introduced the method of isolation of individual cells in 1907. The first important attempt to collate the facts and discuss them in relation to genetic theory was that of Pringsheim (1910). In 1912 Beijerinck treated in considerable detail the problems of "mutation" and "atavism" in

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, Aug. 18, 1926.

micro-organisms (compare also his very interesting paper published in 1900) and important studies were issued by Baerthlein (1912), Burgeff (1912, 1914, 1915), Schiemann (1912), Watermann (1912, 1913), Dobell (1913), and Schouten (1913, 1914). Since this period which marks the real beginning of critical interest in these problems numerous researches have been carried out and our knowledge has increased greatly.

During the last few years the facts in different portions of the field of work have been compiled and discussed by various authors. The data of bacterial variation have been considered by Baerthlein (1918), Adami (1918), Gurney-Dixon (1919), Schmitz (1919), Toenniessen (1921), Löhnis (1921, 1923), Bergstrand (1924), Janke (1924), Enderlein (1925), Almquist (1925), and von Niessen (1926). Many references and discussions of the cytological bases of fungal genetics will be found in Tischler (1921, 1922) and in Gäumann's (1926) recent volume. Guilliermond (1920) and Lindner (1922) have considered the yeasts. Data on the *Erysiphaceae* have been collated by Zimmermann (1924) and Hammarlund (1925). Literature on the rust fungi has been brought together by Zimmermann (1925) and by Ducomet and Foex (1925); see also Dodge and Gaiser (1926). The smut fungi are discussed by Sartoris (1924), Bauch (1925), and Blizzard (1926). Data on the *Zygomycetes* have been brought together by Burger (1919), Blakeslee (1920), Namylowski (1920), Cutting (1921), and Burgeff (1914, 1915, 1924) and on the *Basidiomycetes* by Bensaude (1918), Kniep (1923), Brunswik (1924), Zattler (1924), Vandendries (1924, 1925), Hanna (1925), and Newton (1926). The data on variation in other groups of fungi have not yet been collated, but references and discussions will be found in Haenicke (1916), Schiemann (1918), Stevens (1922), Brierley (1919, 1920, 1922), La Rue (1922), Blochwitz (1923), Janke (1924), Leonian (1925), Christensen (1925), Brown (1926), Thom and Church (1926).[2]

The above publications and their bibliographies give an outline of the present position of the genetics of fungi and bacteria. In many researches the main interest of the investigator has been primarily clinical, physiological, or directed to some other aspect, and essential genetic criteria have often been overlooked, or the facts of variation have not been recorded with sufficient accuracy and detail. In consequence many data of the greatest interest have little evidential value for our particular purpose.

The aim of this paper is to survey broadly the present position of genetic study in mycology and bacteriology, and to consider how the problems relate to those in other groups of organisms and to fundamental concepts of genetic theory. No attempt is made to give a complete citation of literature and only such work is referred to as illustrates the point of view I have put forward or gives access to the further literature of the subject. Consideration of all the evidence available has led me to adopt this viewpoint which, I believe, gives the truest perspective and balance of values in this field of work.

[2] Since this paper was read at the International Conference of Botany, F. Chodat (1926) has published an account of morphological and physiological variation in *Aspergillus ochraceus* and *Phoma alternariacearum.*

B. Brief Critique of Genetic Phenomena, Concepts and Terminology in Groups of Organisms Other than Bacteria and Fungi

From the point of view of this discussion the main ideas that emerge from the genetic experience of the last 25 years in general biology, as I read the data, may be summarised as follows:—

1. The fundamental value of the pure-line concept; the constancy of the pure-line; the inefficacy of selection within the pure-line and the fact that whenever selection has seemed effective later work has thrown doubt upon the genetic purity of the stock, or has proved it to be a population in which strains were being selected.

2. The value of Baur's (1914) classification of variations into the three categories: (1) *modifications*—non-heritable differences caused by environmental conditions; (2) *combinations*—heritable differences caused by segregation and recombination of hereditary units of two kinds, (a) normal segregation and recombination, (b) aberrant segregation and recombination; (3) *mutations*—heritable differences which do not depend upon segregation or recombination.

3. That all genetic experience has proved these three categories to form a hierarchy of values;[3] that is, that all variations are to be regarded as modificatons until they can be proved to be combinations, and as combinations until they can be proved to be mutations. "Combinations" cannot be distinguished from "mutations" by observation but only by precise factorial analysis. The majority of the variations to which the term "mutation" has been loosely applied are more correctly interpreted as "combinations" (see Lotsy, 1916–1925, Heribert Nilsson 1920, Blakeslee 1921, Bateson 1925, Morgan 1925, 1926). The loose usage of the term "mutation" implies little if anything more than the words "discontinuous variation" and in this connotation the former term seems unnecessary. In fact, for all purposes of exact study and discussion of variation, some scheme of classification such as that proposed, for example, by Bridges (1923) must be adopted. It is then clear, that the whole tendency in critical genetic work is to confine the term "mutation" to the "transgenation" of Bridges or the "point mutation" of Morgan, and logically this would appear to be the only sound position. This leads to the following definition of mutation: "The result of a change in genotypic constitution occurring independently of normal segregation, crossing-over, or irregular chromosome division; strictly, an alteration in the fundamental nature of the germplasm, usually in a single gene" (Jones 1925). The more recent researches on variation in apomictic forms would appear to emphasize the truth of Lotsy's (1916) dictum—"certainty of purity however is a *conditio sine qua non* to obtain proof of the existence of mutation in living beings, just as chemical purity is a *conditio sine qua non* to obtain proof of the existence of mutability of the elements. "Mutation" is, in fact, the ultimate category in biology as it is in physics and chemistry. The extreme difficulty of proving purity of genotype is well exemplified by the work

[3] "Essentia non sunt multiplicanda praeter necessitatem." William of Occam.

of Noack (1924, 1925), Bateson (1926) and others on somatic segregation and by the attack that has recently been made by Jeffrey, and Jeffrey and Hicks (1925) on the *Drosophila* foundations. (See also Lotsy 1919–1922.)

4. The particulate, determined nature of hereditary relationships and the extreme rarity in "mutation" of the phenomenon of reversion. The latter is frequent in combinations and perhaps even the few recorded cases of reverting "mutations" may be explicable in terms of crossing over (Sturtevant 1925), or some other mode of re-ordering existing "units."

C. Consideration of Fungi and Bacteria

The fungi, and still more the bacteria, are usually regarded as exceptional or aberrant groups of plants to which the genetic concepts derived from the study of other groups of organisms do not apply. In certain cases this view is based upon philosophic ideas of what constitutes an individual or generation (Northrup 1920, van Loghem 1921, etc.), but the more usual ground of objection is the presumed absence of sexuality. It is of course possible to consider separately any group of organisms and to develop within its own boundaries conceptual structure and terminology. In such case, terms already pre-empted in the wider field should not be used with a different connotation in the narrower field, for the equation of similar terms crystallising different concepts only leads to chaos.

The whole history of genetic study has, however, shown a more and more widely-embracing scope for its fundamental concepts and an ever-increasing range of application for its criteria and terminology. In no other field of biology, perhaps, has the comparative method so fully proved its value. In the animal world the protozoa alone among the groups studied from this point of view, seemed for a time to stand isolated, but as Calkins' (1926) has shown (see also La Rue 1922), the protozoal data fall into line with those of other groups. It is of considerable interest that Calkins only accepts one case as a "true mutation," and this is of a type that most geneticists (see for example Baur's classification or Blakeslee 1921), might class as a "combination." In the plant world the data from phanerogams and pteridophytes are conformable, the recent work of Wettstein (1924) and Allen (1924, 1925, 1926) have shown the agreement of the bryophytes, and what little evidence there is on the algae falls into line.

As I read the data, the investigations of the last few years show clearly the possibility of applying the fundamental concepts, criteria, and terminology of genetics to the last remaining groups, the fungi and bacteria.

D. Classification of Data on Variation

In order to deal with the facts of variation in bacteria and fungi it is necessary to classify them, and this may be done in two ways. One may follow Pringsheim (1910), Gurney-Dixon (1919), and nearly all other writers on this subject and arrange the data according to the phenotypic nature of the variation, for example, changes in morphology, in colony formation, in optimum temperature,

in fermentation powers, in color formation, in virulence, and so forth. This method is convenient for laboratory reference and provides valuable information regarding scope and direction of variation, but it gives little of genetic value. On the other hand one may arrange the facts according to the time and mode of origin of the variants, their constancy and relation to environmental conditions and their relation to prior and succeeding generations (see, for example the summary in Haenicke 1916). This ordering of data cuts right across the first method for, in it, the phenotypic nature of the variation is immaterial. In a careful study and comparison of the available data arranged according to Pringsheim's (1910) schedule, extended to include additional phenotypic values, with the same data arranged in the schedule outlined below, I have been able to trace no correlations that seem to me to possess noteworthy significance. Variations have been described in practically every recognisable character of fungi and bacteria, and although in certain cases there are indications of "linked" or grouped variation, the evidence is yet too meagre to permit of a considered opinion. In the outline which follows I have arranged some of the more recent data. Many important references are omitted because the author has not given necessary details or, in certain cases, because I have been unable to consult the paper. On the other hand, many authors will no doubt feel that I have taken liberties in my interpretation of their results.

E. Outline Scheme of Classification of the Data of Variation on Genetic Criteria

(1) Modification, non-heritable differences caused by the unequal influence of different conditions and varying immediately with the conditions. *Examples*—universal throughout fungi and bacteria.

(2) Continuous Variation, heritable differences characterised by the gradualness of the change through successive generations.

I. *Adaptive Variation*, in which the nature and direction of the change bears an adaptive relationship to the conditions under which the change appears, for example, a non-starch fermenting organism, which, grown on a medium containing starch, "acquires" gradually the capacity to ferment starch.

a. *Reverting Variation*,[4] in which a character gradually appearing during a tendency of conditions gradually disappears when the tendency of conditions is reversed.
   Examples. Harden & Norris (1910), Klein (1912), Baerthlein (1912–1918), Adami (1918), Ledingham (1918), Cooper (1919), Richet and Cardot (1919), Zikes (1919, 1920), Blunck (1920), Grushka (1920), Toenniessen (1921), Mellon (1921), Morishima (1921), De Kruif (1921, 1922), Felix (1922), Walker (1922), Jungeblut (1923), Rosenow (1923), Sanfelice (1924), Stuart (1924), Bresciana (1924).

b. *Non-reverting Variation*,[5] in which a character gradually appearing during a tendency of conditions remains when the tendency of conditions is reversed.

[4] In certain cases the whole colony is described as showing reversion and, in others, only certain individuals within the colony. In the latter case if the parent colony is growing on a plate the reversion may appear in the form of a sector, secondary colony, etc. (see page 1647).

[5] See Gurney-Dixon (1919) and Löhnis (1921) for criticisms of permanence of variation; Caldis and Coons (1926).

Examples, Hansen (1900), Barber (1907), Sanfelice (1912), Henri (1914), Jordan (1915), Adami (1918), Baerthlein (1912–1918), Wehmer (1919), Grushka (1920), Fabry (1921), Botez (1922), Stuart (1924), Harms (1924), Cardot and Laugier (1925), Goyle (1926).

II. *Non-adaptive Variation*, in which the nature and direction of the change bears no apparent adaptive relationship to the conditions under which the change appears, for example, a color-forming organism which grown in culture gradually "loses the capacity" to form color.

a *Reverting Variation*, in which a character gradually appearing during a tendency of conditions gradually disappears when the tendency of conditions is reversed.

Examples, Bernhardt and Markoff (1912), Appel and Wollenweber (1913), Heinemann (1917), Baerthlein (1918), Prell (1918), Butterfield and Neill (1920), Jordan (1920), Meyer and Neilson (1920), Dastur (1920), Burger (1921), Vandremer (1921), Fürth (1922), Bergstrand (1923), Breinl and Fischer (1923), Orcutt (1923), Burkholder (1923, 1925), Hersfield and Zajdel (1924), Oehlkers (1924), Thom and Church (1926).

b. *Non-reverting Variation*, in which a character gradually appearing during a tendency of conditions remains when the tendency of conditions is reversed.

Examples, Lindner (1909), Euler and Svanberg (1919), Manniger (1919), Van Loghem (1919), Cranstedt (1920), Dastur (1920), Jordan (1920), Fürth (1922), Breinl and Fischer (1923), Hersfield and Zajdel (1924), Blochwitz (1925), Thom and Church (1926).

(3) *Discontinuous Variation*, heritable differences characterised by the suddenness of their appearance.

I. *Adaptive conditioned Variation* in which a character appears under definite conditions and bears an adaptive relationship to those conditions, for example, a non-starch fermenting organism which, grown on a medium containing starch, "acquires" suddenly the capacity to ferment starch.

a. *Reverting Variation*, in which a character suddenly appearing during a tendency of conditions, suddenly disappears when the tendency of conditions is reversed.

1. *Single*. Variant having appeared once only.

2. *Sequent*, variant giving rise to one or more successive variants in sequence.

Examples, Beijerinck (1912), Baerthlein (1918).

3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.

(i) *Similar*, stock giving rise to the same variant two or more times.

Examples, Beijerinck (1912), Baerthlein (1918), György (1920), Vandremer (1921), Toenniessen (1921).

(ii) *Different*, stock giving rise to different variants.

Examples, Baerthlein (1918), Blake and Trask (1923).

b. *Non-reverting Variation*, in which a character suddenly appearing during a tendency of conditions remains when the tendency of conditions is reversed.

1. *Single*, variant having appeared once only.

Examples, Richet and Cardot (1919, 1920).

2. *Sequent*, variant giving rise to one or more successive variants in sequence.

3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.

(i) *Similar*, stock giving rise to the same variant two or more times.

(ii) *Different*, stock giving rise to different variants.

II. *Non-adaptive conditioned Variation*, in which a character appears under definite conditions, but which bears no apparent adaptive relationship to those conditions, for example, a color-forming organism which, grown on a particular medium, suddenly loses the capacity to produce color.

a. *Reverting Variation*, in which a character suddenly appearing during a tendency of conditions suddenly disappears when the tendency of conditions is altered.

1. *Single*, variant having appeared only once.

Examples, Haenicke (1916), Chaudhuri (1924).

2. *Sequent*, variant giving rise to one or more successive variants in sequence.

Examples, Haenicke (1916), Felix (1922).

3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.

(i) *Similar*, stock giving rise to the same variant two or more times.
   Examples, Sachs-Müke (1913), von Lingelsheim (1913), Kakehi (1916), Haenicke (1916), Gorini (1921), Toenniessen (1921), Leonian (1925).
(ii) *Different*, stock giving rise to different variants.
   Examples, Scales (1921), Christensen (1925).

b. *Non-reverting Variation*, in which a character suddenly appearing during a tendency of conditions remains when the tendency of conditions is altered.

1. *Single*, variant having appeared once only.
   Examples, Henri (1914), Haenicke (1916), van Loghem (1919), Leonian (1925).
2. *Sequent*, variant giving rise to one or more successive variants in sequence.
   Examples, Haenicke (1916), Schmitz (1919), Felix (1922), Ørskov and Larsen (1925).
3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.
   (i) *Similar*, stock giving rise to the same variant two or more times.
      Examples, Eisenberg (1913), Haenicke (1916), Gorini (1921), Toenniessen (1921), Kniep (1923), Blochwitz (1923), Krumwiede, Cooper and Provost (1923).
   (ii) *Different*, stock giving rise to different variants.
      Examples, Schiemann (1912), Eisenberg (1914), Mackie (1920), Heller (1922), Blanc (1923), Christensen (1925), Brown (1926).

III. *Non-adaptive unconditioned Variation*, in which a character appears under different conditions, but which bears no apparent relationship to those conditions, e.g., a colorless organism which under various conditions may suddenly develop the power of producing color.

a. *Reverting Variation*, in which a character suddenly appearing is suddenly lost, the changes showing no apparent relation to external conditions.

1. *Single*, variant having appeared once only.
   Examples, Shear and Wood (1913), Burgeff (1915), Blakeslee (1920), Stevens (1922), Dickson (1925).
2. *Sequent*, variant giving rise to one or more successive variants in sequence.
   Examples, Baerthlein (1911), Biejerinck (1912), Toenniessen (1914), Kakehi (1916).
3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.
   (i) *Similar*, stock giving rise to the same variants two or more times.
   Examples, Arkwright (1921), Gorini (1922), Mellon (1922), Leonian (1925), Balteanu (1926).[6]
(ii) *Different*, stock giving rise to different variants.
   Example, Gratia (1921).

b. *Non-reverting Variation*, in which a character suddenly appearing remains permanently, the change showing no apparent relation to external conditions.

1. *Single*, variant having appeared once only.
   Examples, Edgerton (1908), Grossenbacher and Duggar (1911), Shear and Wood (1913), Brierley (1920), Blakeslee (1920), Stevens (1922), Almquist (1922), La Rue (1922), Blochwitz (1923), Bonar Lee (1924), Dickson (1925), Crowell (1926).
2. *Sequent*, variant giving rise to one or more successive variants in sequence.
   Examples, Stevens (1923), Brown (1926).[7]
3. *Recurrent*, stock giving rise to several variants either simultaneously or consecutively.
   (i) *Similar*, stock giving rise to the same variant two or more times.
      Examples, Crabill (1915), Guilliermond (1920), Matsumoto (1921), Arkwright (1921), Toenniessen (1921), Kursanov (1922), De Kruif (1923), Brown and Horne (1924), Mellon (1925).
   (ii) *Different*, stock giving rise to different variants.
      Examples, Crabill (1915), Feldmann (1917), Schouten (1918), Burger (1921), Seiffert (1922), Heller (1922), Stevens (1922), Roberts (1924), Brown and Horne (1924), Brown (1926).

[6] F. Chodat (1926).
[7] F. Chodat (1926).

F. Terminology of Classification

The above classification is purely tentative and is a preliminary attempt to bring some kind of genetic order into the data of variation in bacteria and fungi. With additional and more accurate data the variations might be further classified into changes in one character, in several unrelated characters, or in groups of characters; changes in all the individuals of a colony or only in a greater or lesser number; changes at regular, cyclical, or irregular intervals, and so forth, but the suggested scheme appears to go as far as present data permit.

Many different names have been used by writers to describe the changes they have noted. Both continuous and discontinuous changes have been referred to as "impressed variation," "adaptation," "clone-formation," "accoutumance," "inheritance of acquired characters," "enduring modification," "fluctuation," "training," "education," "saltation," "transmutation," "mutation," "sport," etc. Most writers have not defined the sense in which they have used any particular term, or in many cases definitions that have been given are mutually incompatible; often the different classes of variation have not been distinguished and quite frequently the one term has been used by an author to describe very different types of variation. Much controversy has centered in particular around the concept "mutation" and the usage of the term, although problems of "mutation" cannot be treated independently of the more general questions of variation. Brown (1926) has recently asserted that "it is obvious that this word (mutation) has been used by mycologists and bacteriologists" for "sudden changes which are neither the result of a process of gradual acclimatization or 'education' "[8] nor of selective isolation, and that "this is the only sense in which the term 'mutation' can be applied as yet in microbiology." As early however as 1913 Dobell found cause to deplore the fact that "the word 'mutation' has been used with such different meanings by so many bacteriologists and others" that much of this controversy "might have been avoided in many cases if the opponents had defined their use of the word precisely." In the numerous papers published since 1913 the controversy has become more involved, and, if one reads this literature, one finds that the term "mutation" has been used explicitly to connote all the main types of continuous and discontinuous variation outlined in the schedule scheme. Owing to the confusion and misconceptions to which the almost indiscriminate use of this term has given rise (by reason of the fact that it has not connoted any clearly defined concept) many workers on bacteria and fungi have urged that the term should not be used in the study of these organisms. (See Haenicke 1916, Schiemann 1918, Morishima 1921, van Loghem 1921, Brierley 1922, Jollos 1924, Ørskov & Larsen 1925 etc.) "Saltation," the word adopted by Stevens (1922) suffers from similar disabilities, having been used by Darwin and many of the older workers in different senses. It had, however,

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[8] Compare, for example, Adami, 1918, in the bacteria mutations are impressed "variations" and this is illustrated by examples of the gradual acclimatisation or "education" of bacteria to ferment sugars, etc.

largely become obsolete, and so has not entered the field of controversy to the same extent as "mutation." The difficulty is to describe particular phenomena briefly and objectively. Terms imply particular concepts or interpretations and, it is not so much the term which matters, as the concept which is crystallised in it. If the term used is itself ambiguous, confusion is inevitable.

The "practical student of fungi and bacteria," content to record empirical data and taking little or no interest in the philosophy of his subject, often considers insistence on exact terminology to be mere pedantry. The history of scientific thought, however, both in general and in particular shows clearly the necessity for the crystallisation of distinct concepts in specific and unambiguous terms, and much scientific advance not only depends upon but *is* increasing exactness in terminology. Nowhere is this more strikingly shown than in the field of genetic research and, in perhaps no problem so much as "mutation," is it more necessary, or has its absence given rise to greater misconception and controversy. (See Bernhardt 1913, Haenicke 1916, Schiemann 1918, Gurney-Dixon 1919, Heribert Nilsson 1920, Blakeslee 1921, Prell 1922, Lotsy 1922.)

Until data are forthcoming which will allow of the formulation of precise concepts it would seem best in our field of study, to use the comprehensive and non-committal terms "variability," "variation" and "variant," and to define these more exactly by prefixing one or more adjectives such as "continuous," "discontinuous," "conditioned," "unconditioned," "reverting," "non-reverting," "adaptive," "non-adaptive," and so forth.

The data of variation taken at their nominal value which, in numerous cases, is obviously not their true value, present great resemblances to the data of variation in general, if both are arranged as shown in the tentative scheme. Modifications are universal. The variations classified under (2) and (3) show analogies to those which in general genetics have proved to be due to selective elimination. (Compare Jennings 1926.)[9] The variations classified under (3) II and (3) III show analogies to the phenomena of variation exhibited by the *Oenothera* complex, bud sporting, etc. These analogies however, exact and suggestive as they appear when viewed in the historical perspective of genetic theory, are only analogies, and seem to fail when it is stated that in bacteria and fungi the variations arise in the progeny of asexual single organisms. In actual fact the greater number of studies have not been carried out on single-cell cultures, but during the last few years this has been done sufficiently often to leave little doubt that most, if not all, of the types of variation noted can occur in the progeny of single organisms. Nominally such cultures are "clones," and, if sexuality be absent, the "clones" are presumed to be genetically pure. The evidence leaves little doubt that in such presumably "genetically pure clones" selection may be effective in a greater or lesser number of generations, or spontaneous changes of various kinds may occur, some of which are apparently

[9] It is interesting to note that, referring to *Drosophila*, Morgan (1926) states, "Some of the mutant stocks have, after a time, seemed to lose more or less the characteristics of that stock, yet when outbred it has been found that the mutant character can be recovered in its original strength."

permanent, whilst others may revert. If this truly represents the position in the bacteria and fungi then the fundamental concepts of genetics are inapplicable to these groups, which would seem to stand alone in the organic world. On *a priori* grounds, this would be so striking a position, that a sceptical attitude would be justifiable so long as any possibility of doubt remained and, in the historical and comparative perspective, every source of error would acquire increased value.

In the remaining portion of this paper I shall endeavor to show not only that such sources of error and doubt are manifold, but that all recent studies tend to suggest the probability that fungi and bacteria will prove susceptible of common genetic interpretation.

G. Discussion of the Bases of Variation in Fungi and Bacteria

I. CYTOLOGY OF FUNGI AND BACTERIA

A widely held opinion, even among competent workers, is that as amitosis is prevalent in fungi and as nuclei in the bacteria have "little more than hypothetical existence" (Brown 1926)[10] one cannot expect in these groups the precise and causal genetic relationships which prevail in higher forms—this, in spite of all common experience that genotypic constancy of a meticulous order and extending through innumerable generations is the rule rather than the exception in these groups.

Examination of the evidence shows that in practically all recent or critical studies the intimate structure of the fungal nucleus and its behavior during mitosis are fundamentally like those in other plants (see Tischler 1921, 1922, or for good and more recent examples, Bagchee 1925, or Bauch 1926) and that amitosis is conspicuous by its absence.[11] Claims of amitotic behavior, save perhaps in certain abnormal or degenerating cells, in my opinion, require confirmation. With regard to the bacteria a number of cytological studies have appeared recently in which nuclei or nucleus-like bodies of rather variable form with, in certain cases, appearance of simple mitotic behavior, have been described. (Paravicini 1918, Schussnig 1920, Kirchensteins 1922, 1923, Awerinzew 1924, Almquist 1925, Enderlein 1925, Gutstein 1925, Bessubetz 1925, etc.[12] (See also the earlier workers such as Meyer 1910, Dobell 1911, etc.) Even, however, if one knew nothing of the cytology of these forms, the genetical data available would necessitate the formulation of a behavioristic hypothesis of some comparable exact mechanism of heredity just as, knowing nothing of the

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[10] Compare Hiss-Zinsser and Russell (1922). "The presence of a *nucleus* in bacterial cells though denied by the earlier writers, has been demonstrated beyond question."

[11] Perhaps the best recent case is that described by Smith (1923) in hyphae of *Saprolegnia* but this bears striking resemblances to simplified mitotic phenomena in the karyosome nuclei of Protista and the work was carried out on fixed and stained unsectioned material using very high magnifications (×3000). The nuclear behavior in yeast budding (Guilliermond 1920, Fuhrmann 1926) should be compared with the recent studies of Nadson and Konokotine (1926) on *Nadsonia*. (See also Conklin 1917, Sakamura 1920, Tischler 1921, 1922, Wilson 1925, Sharp 1926.)

[12] See also the recent paper by Rosen (1926).

structure or appearance of the "gene," Morgan (1926) has yet formulated a theory of it.

Naturally the fungi and bacteria may be expected to show "local" peculiarities, as do most other groups of organisms (Tischler 1921, 1922). For example, the multinucleate condition of many fungi with wall formation independent of nuclear division, and the various methods of reproduction in both groups must modify their genetic processes, but, in general, there seems no reason deriving from our present knowledge of cellular structure why one should not expect the fundamental concepts of genetics to apply to these groups just as, with local modifications, they seem to apply to the protista, bryophyta, etc.

II. IMPURE GENETIC MATERIAL

Many variation data are valueless or greatly reduced in value because adequate precautions were not taken to ensure absolute purity of the original culture, a fact pointed out by many workers. (Gurney-Dixon 1919, Heller 1922, Calmette 1924, etc.) All more recent critical experience demonstrates the frequency and tenacity with which infinitesimal numbers of one organism may persist, sometimes apparently for years, in "pure cultures" of another organism and are only revealed by special or selective technique. Several transfers from single colonies on plates or hosts may not eliminate this initial "contamination" which may only become apparent under some particular circumstance. The only safe procedure is the isolation of single individuals, single hyphal tips or spores, and in critical genetic study such a procedure is imperative, for the very basis of genetics is continuous individual study. In bacteriology, particularly, more investigations such as those of Hort (1920), Gardner (1925), etc., in which the intimate development of single individuals are followed, are greatly to be desired.

A second source of error is recontamination of pedigreed cultures—a danger which, as Löhnis (1922) indicates, may be increased by single-cell technique. Workers are apt to disclaim the possibility of this error in their personal researches, but it is simply the outcome of experience that even the best investigators using the most faultless technique suffer occasionally from contaminated cultures. Usually, such recontamination is obviously due to invasion but in other cases it is very easy to interpret the new form as a discontinuous non-reverting variation or, if the new and initial strains establish an equilibrium, to find in this the experimental basis of continuous variation according as one or the other component is selected by the conditions. (Cole and Wright 1916, Schade 1919, Brierley 1919, 1922.)

Much of the earlier work on variation in the rust fungi, powdery mildews, and yeasts, and a considerable number of even more recent studies on bacterial variation are, I think, clearly to be considered as examples of a lack of genetic purity in the subject material. It is in regard to cultural results having origin in this source of error that Emerson (1922) may perhaps be quoted:—"The possibility of overlooking even prominent variations until they have once been noted, together with the readiness with which they are found after one's at-

ention has been focussed on them will hardly be questioned by anyone who has given attention to the discovery of new variations in almost any organism."

III. CYCLICAL DEVELOPMENTS IN FUNGI AND BACTERIA

A fundamental criticism of the commonly accepted interpretation of the facts of variation in bacteria and fungi is steadily becoming clearer as researches of the last few years on life cycles, ontogenetic stages and other cyclical developments are becoming known and their implications realised. Already the known complexity of development in vegetative and reproductive phases and the genetic complications which ensue necessitate a complete re-orientation of our attitude regarding these groups of organisms. This work will be briefly considered from a comparative point of view in the following pages.

1. PHYSIOLOGICAL DIFFERENCES IN INOCULA

Inocula of different physiological condition, from young or from old cultures, from aerial or from submerged growth, from vegetative or from reproducing growths, etc., may give rise to variations in the progeny which usually immediately revert but which, apparently, may persist under particular conditions, for a greater or lesser number of generations. This has frequently been described in bacterial culture (Mellon and Anderson 1919, Clark and Ruebl 1919, Toenniessen 1921, Henrici 1921, Churchman 1921, Sherman and Albus 1923, etc.) and my own experience agrees with that of Waksman (1919), Lieske (1921), and others, that it is a serious technical difficulty in studying Actinomycetes. Its occurrence in fungal cultures has been suggested by Appel and Wollenweber (1910), Blochwitz (1923), Leonian (1925), Brown (1926), and others. Cayley's (1923) interesting results should also be noted. The correlation of physiological changes with age (and possible correlation of this with nuclear rearrangements or intersexuality due to a changing enzymic balance) described by Vandendries (1924), Newton (1926), and Gilmore (1926), is particularly suggestive in comparison with Burgeff's work on *Phycomyces* and *Absidia* (1914, 1915) and with Blakeslee's results (1920), and it would seem possible that some such cytological basis may underlie the physiological appearance.

My own experience with fungi is that physiological differentation often of a transient nature, occurs not infrequently. Certain strains of *Botrytis cinerea* for example, in Raulin's solution produce aerial conidial hyphae of *Polyactis* type and submerged micro-conidial hyphae.[13] Transfers from the former repeat the general condition, but transfers from the latter may at times give only micro-conidial hyphae for a varying number of sub-cultures, after which they again produce the general condition. At any time apparently micro-conidial hyphae produce conidia of *Polyactis* type if transferred to a solid medium. Further, in

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[13] Micro-condidia or micro-sporidia, which are formed by a great number of fungi and are found to be extremely common when looked for, are a spore form about which practically nothing is known, and yet which, from the manner of their formation, may have considerable genetic interest. In many forms such as *Botrytis*, *Fusarium*, *Helminthosporium*, etc. a conidium, on germination may give rise directly to one or sometimes two or more clusters of micro-conidia in lieu of a germ tube, so that the resulting culture might perhaps be regarded as of multisporous origin.

examining a large number of different soil fungi over a period of several years, I have been impressed strongly by the fact that in many cases a conidial transfer may give rise primarily to conidial growth and a hyphal transfer to vegetative growth, and that one may get 'runs' of vegetative growth alternating irregularly with 'runs' of sporogenous growth. I am inclined to think that this physiological gradience or perhaps cyclical development (compare Calkins 1926, on the Protozoa), may in fungi, and possibly in bacteria, be more prevalent and fundamental than is usually appreciated, although as such work has rarely been carried out with single individuals or single spores, the results may simply be due to selective elimination: its bearing on the technique of the study of variation in these groups will be obvious.

2. LIFE CYCLES AND ONTOGENETIC STAGES

Arising out of the foregoing, but having more serious relation to our problem, are the newer researches on the normal life-cycles of micro-organisms. The possible complexity of the fungal life-cycle is too well known to need emphasis and all I would indicate is its relation to the question discussed above and the fact that practically nothing is known of the relative genetic value of the several spore forms within any one life cycle. One may suggest, however, that single-spore cultures may not be of equal genetic value—compare, for example, a uninucleate unicellular spore such as *Thielavia basicola*, a multinucleate unicellular spore such as *Aspergillus herbariorum* or *Botrytis cinerea* and multicellular spores, with, as a rule, uninucleate cells such as *Fusarium sp.*, *Helminthosporium sp.*, etc. Also a culture originating in a fragment of mycelium, hyphal tip, etc, may, in certain cases, as for example smut fungi, Hymenomycetes etc., be very different genetically from one developing from a single spore.

So far as the bacteria are concerned the view still generally held, that these organisms reproduce entirely by simple fission or single endospore formation, would seem to be no longer tenable. Much of the recent work has been collated and discussed by Löhnis and Smith (1916, 1923) and by Löhnis (1921); but the following references should also be consulted,—Mellon (1920-1926), Almquist (1922-1925), Potthof (1922), Bergstrand (1918-1924), Enderlein (1925), Schmitz (1919), Tunnicliff (1923), Rosenow (1923), Lantzsch (1922), Zlatogorof (1922), Lieske (1922), Gorini (1922), Dostal (1923), Hort (1920), Janke (1924, Gardner (1925), Levine (1925), Stearn, Studivant and Stearn (1925), Ørskov (1925), Fuhrmann (1926), von Niessen (1926), Thornton and Gangulee (1926), etc. For the present discussion the important points are not only that many bacteria possess a complicated life-cycle the stages of which may show distinctive morphological and physiological characters, but that, for a greater or a lesser number of generations, individual 'ontogenetic stages' may apparently reproduce as such, maintaining their distinctive characters. This phenomenon is well-known in other groups of animals and plants, but its recognition is fundamental and almost revolutionary in the study of bacterial variation. There can, I think, be little doubt that a great part of the literature on variation in bacteria deals simply with the passage of one 'stabilised' developmental phase into one or

more others.   The scope of the changes described illustrates the flexibility of bacterial organisation and broadens the limits within which modification may occur (compare recent views on the protozoa, Calkins 1926).   Sherwood (1917) writing of pleomorphic streptococci sums up the position well in saying, "I feel that a healthy skepticism is well worth while in all work involving mutation, since errors in technique can lead to very erroneous conclusions."

A further complication which may more or less seriously affect our problem is the suggestion to which evidence points, that the conditioning of stages in bacterial life-cycles and the appearance of variants may bear relation to the activity of the bacteriophage. (Davison 1922, Bergstrand 1922, D'Herelle and Handmoy 1925, D'Herelle 1926, Ørskov and Larsen 1925).

3. SEXUALITY AND ITS COROLLARIES

Quite fundamental to our subject are the researches of the last ten years or so on sexuality in fungi and bacteria.

a *"Sexuality" in bacteria.*   In a recent paper Brown (1926) speaks of "bacteria in which no process of fusion of any kind has ever been observed," and this is still a common opinion.   Some years ago (Brierley 1922), a critical and detailed examination of such evidence as was available in the literature of bacteriology led me to the point of view that, in the absence of some process of fusion and segregation, bacterial variation presented an apparently unresolvable chaos. On the other hand "granting the assumption of the occurrence in bacteria of genetic impurity with some mechanism of segregation, all the data concerning variability and apparent mutation in this group fall astonishingly well into line with modern genetical conceptions" (Brierley 1922).   During the last few years, direct evidence of fusion between bacterial cells has steadily accumulated, and if one impartially studies these data, it is difficult to oppose the view that the occurrence of cell-fusions followed in certain cases by the formation of various types of reproductive body has been demonstrated. (See Löhnis and Smith 1916, 1923, Löhnis 1921, Schmitz 1919, Schussnig 1920, Lieske 1922, Potthoff 1922, 1924, Almquist 1925, Enderlein 1925, Mellon 1923-6, etc.)   Almquist (1924–1925) claims to have hybridized experimentally two bacterial species, B. *typhi* and B. *dysenteriae* with the production of a new form, B. *diploides.*

This is not the place to enter into an exact evaluation of the weight of evidence for this or that detail in this mass of work; it is only germane to our discussion that cell-fusions giving rise to reproductive bodies and determined growth have been shown to occur in the bacteria.   This throws open in this group the whole field of problems originating in 'syngamy' or 'amphimixis' and brings within view the possibility that the bacteria conform with other groups of animals and plants in which the phenomena of variation are fundamentally related to processes of 'combination' and of 'segregation.'   Many bacterial data for which, on account of the definiteness and regularity of the appearance of specific variants no acceptable explanation has been forthcoming, would, in the light of this hypothesis, be examples of fairly simple processes of segregation from genetically complex parentage (Kakehi 1916, Baerthlein 1918, Schmitz

1919, Jordan 1920, Arkwright 1921, Toenniessen 1921, Botez 1922, Brierley 1922, Krumwiede, Cooper and Provost 1923, Blake and Trask 1923, Stuart 1924, Gardner 1925, Ørskov and Larsen 1925, Crowell 1926, etc.)[14] Further, in the clone that might result from a single genetically impure parent, selective elimination would give rise to all the phenomena of apparently continuous variation. (Cole and Wright 1916, Brierley 1919, 1922).

In view, therefore, of the work of the last ten years on bacterial cell-fusions or 'cyclogeny' and of life-cycles, and in view of the sources of error that have been pointed out which make possible interpretations alternative to those usually accepted, it would seem premature to regard the bacteria as an entirely aberrant group to which the fundamental concepts of genetics cannot apply (Schiemann 1918, van Loghem 1921, etc). Further, it would seem premature whether from a theoretical or a pragmatic standpoint to interpret any of the described variations as other than 'modifications' or 'combinations'. This is not to assert that 'mutations' in the strictest sense may not occur in the bacteria, or that its occurrence may not be abundantly proved when factorial analysis becomes possible, but it is to state the definite opinion that there is yet no evidence which compels one to believe that it does occur.

b *Sexuality in fungi.* Most of the earlier workers on sexuality in the fungi were concerned with the demonstration of the existence of this process and, so numerous are the records and so wide the field covered, that the prevalence of sexual fusions in all groups of fungi is now accepted. This work actively continues, asexual spore forms being related to sexual stages, or sexuality being demonstrated in forms in which previously it was unknown. So remarkable has been this development during the last twenty-five years that probably no mycologist would assert that, given certain conditions, the possibility of sexuality is absent from any fungus.

Furthermore, two of the most interesting developments in the more recent work have been the demonstration of the widespread occurrence of heterothallism (see Cutting 1921, Betts 1926)[15] which has been found in all the primary groups and even in the *Myxomycetes* (Pinoy 1921), and the complicated yet precise nature of the sexual process in its genetic relationships. The actual occurrence and apparently wide-ranging character of strain and species crossing with all its corollaries throws open the entire scope of critical analysis of fungi on a basis of exact genetic criteria. This field of work seems to me by far the most important in mycology today. Already, certain of our fundamental conceptions are being modified and new points of view are developing which will have the most profound effect upon mycological theory and upon the practical study of fungi, both in themselves and in regard to their pathological relationships. In this field during the last few years valuable work on the Hymenomycetes has been carried out by Bensaude (1918), Mounce (1922), Kniep (1913–1926), Lehfeld (1923), Brunswik (1924), Vandendries (1923–1925), Zattler (1924), Hanna (1925), Newton (1926) and Gilmore (1926); on the Zygomycetes by Blakeslee (1904–

[14] See also the recent interesting papers by Stewart (1926) and Bruce White (1926).
[15] See also Ramsbottom (1926).

1920), Saito and Naganishi (1915), Orban (1919), Burgeff (1914–1925), and Namylowski (1920); on certain groups of Ascomycetes by Schouten (1918), Effront (1920), Kruis and Satava (1924), Wingard (1925), etc. There is also the interesting possibility of hybridization in rust fungi indicated by Hayes and Stakman (1921), Newton (1922), and Dodge and Gaiser (1926). The work of Bauch (1922, 1923, 1925) and Kniep (1919, 1921) on the smut fungi must also be referred to.[16]

The relation of the sexual process to variation in fungi has been almost entirely neglected, chiefly because sexuality has been regarded as strictly autogamous. The widespread occurrence of heterothallism and certain possibilities that will be discussed later give, however, opportunity for the more or less frequent introduction of genetic complexity, which is the primary basis of genetic inconstancy and the occurrence of variation. Even in purely autogamous forms there may occur possibilities of nuclear reorganisation (Bridges 1923, Prell 1922, Tischler 1922, Wilson 1925, Sharp 1926), and these possibilities are multiplied by the multinucleate condition of many forms and the possibility of nuclear increase, decrease and mechanical separation inherent in the hyphal growth, methods of wall formation and asexual spore production of fungi.

Further, much of our knowledge of the genetics of sexuality in fungi is so recent and aligns so well with the concepts of genetics, both in general and in particular, that any seemingly aberrant processes might well, for the time being, be put on one side in a kind of "non-proven" category[17] or stated in purely descriptive terms, until more experience and data are forthcoming. For example, the sex-reversals or condition of intersexuality that Kniep (1923), Vandendries (1924), and Hanna (1925) (compare also Crabill 1915), observed, and which seemed so striking and definite as individual cases, have been shown in the more recent work of Newton (1926) and Gilmore (1926) to be perhaps a common and characteristic feature of many of these fungi. The *mycelial* segregation of sex (compare Vandendries' 1924–1926 theory of "heterohomothallism") which appears to be the basis of this intersexuality is interesting in relation to the apparently similar results of Burgeff (1914, 1915, 1924) on *Phycomyces* and *Absidia*. Blakeslee and Satina's (1926) use of Manoilov's reaction in this study is also of great interest and promise. So far as these fungi are concerned there is much to be said for Morgan's (1926) suggestion (compare also Brunswik 1924) that the term "self-sterility factor" of East and Mangelsdorf (1925) should be adopted in lieu of the word "sex". In any case, before definite genetic interpretations of purely local status but of very wide implication are placed on apparent "sex reversals" in fungi, the data should be examined very thoroughly in the light of ideas and concepts derived from the study of analogous phemonena in other groups of organisms such as described by Czaja (1921–1924), Goldschmidt (1923), Wettstein (1923–1926), McPhee (1924), Hirata (1924), Schaffner (1925, 1926), etc. See also Sharp (1926) and Morgan (1926).

[16] Kniep (1926) has recently published a further important contribution to this subject recording di- and tri-hybrid fusions.

[17] Beijerinck (1900) suggested the term "aberrances" which would seem peculiarly apt.

In spite of the definite results and apparently clear interpretations of Blakeslee (1920, 1921), the ideas which are crystallising out from the studies on sex-conditioning, noted above, point to the need of further investigation of discrepant results on the nature and constancy of sex in *Mucorineae* reported by Burger (1919), Namylowski (1920), and Burgeff (1914, 1915, 1925). The contradictory accounts of the nuclear processes in zygospore formation are also unfortunate. (See Moreau 1914, Keene 1914, 1919, Baird 1924, etc.)

The mycelial segregation of nuclei in *Psilocybe* (Gilmore 1926) which, the evidence suggests, also occurs in other forms, is interesting in view of the very common production of oidia in Hymenomycetes (Snell 1922). Vigorous cultures[18] of primary and secondary mycelia of *Coprinus fimetarius* if flooded with sterile water give rise to large quantities of oidia, and, in stained suspensions of these, one not infrequently finds single cells with irregular numbers of nuclei. These oidia usually germinate in this multinucleate condition. Further, if one mixes together suspensions of germinating oidia from several strains it is not uncommon to see anastomoses between three or more germ-tubes. Brunswik (1924) has recorded *Coprinus* fruit bodies resulting from a fusion of three mycelia, and other similar cases are known.[19] In view of Gilmore's observations these possibilities of aberrant forms become very suggestive.[20]

As one considers all this recent work on sexuality and hybridization in different fungal groups, and particularly if one keeps in mind results of similar work in other groups of organisms the conviction grows strongly that the genetic relationships in fungi are of a perfectly definite and causal order and are to be formulated in terms of combination and segregation, although these often seem to be of a highly complicated order (Brunswik 1926). Hanna (1925) for example, concludes that "sex in *Coprinus lagopus* is determined by certain factors which segregate out according to Mendelian principles," and Mendelian concepts and terminology are used by nearly all the recent workers on the genetics of the Hymenomycetes. The evidence indicates that they apply equally well to other groups (compare Namylowski 1920). The fungi show their own local modifications, but the fundamental concepts of genetics seem to be increasingly applicable. As in all other groups of organisms, aberrant forms of combination and segregation are seen and possible structural and cytological bases for these have been indicated. There would seem to be little reason to doubt that the facts of variation noted in these researches may be justifiably included in the categories of 'modifications' and 'combinations' and that there is yet no compulsion to introduce the category 'mutation'. For the present, however, it would seem wise to confine description to the use of non-committal terms such as I have used in the classification of variations.

   c *Discussion of certain phenomena related to sexuality in fungi.* 1. *Selection*

[18] Grown for me by Dr. R. D. Rege.

[19] Compare also Kniep (1926) on di- and tri-hybrids in smut fungi.

[20] Compare also the abnormal spores and basidia and the tri- and penta-sterigmatic forms with consequent nuclear aberrations recorded by Buller (1922, 1924) and other authors. These are significant in relation to Bauch's (1926) recent cytological study of two-spored forms.

within the strain. A type of genetic research serving to bring the fungi into conformation with other organisms and to extend to this group the 'pure-line concept,' which is the basis of modern genetics, is the testing of the efficacy of selection within single spore strains. The earlier work on the rust fungi and powdery mildews appeared to show conclusively that the genotype in fungi could be altered by 'training' or 'selection,' and that the 'pure-line' concept was not applicable. The recent work of Stakman and his colleagues (1914–1923), Newton (1922), and others seems, however, to have proved definitely in such rust fungi as have been more critically tested, that the genotype of a single-spore strain is impervious to selection and that apparent variation is due to selective elimination (Mains and Jackson 1926). Hammarlund (1925) has reached the same conclusion with regard to *Erysiphe*. La Rue (1922, 1925), Roberts (1924), Miller (1926), and Ayers (1926) have shown the inefficacy of selection in their particular single-spore cultures of *Pestalozzia* and *Helminthosporium*.[21] In my own experience selection work extending over several years on a single-spore strain of *Botrytis cinerea* has proved entirely useless. The characters studied were size and color of sclerotium and density of conidial production. There have been wide fluctuations from the mode which have often extended over several transfers, but there has been no permanent diversion of strains. An albino variant (Brierley 1920) which appeared once in 1917, and its black parent, are still in continuous parallel culture and, so far as I can test, both have remained absolutely constant in all characters. The 'albino' has not reappeared in over one thousand linear culture-generations and a great number of collateral transfers of the black parent. The uniqueness and constancy of this form is suggestive of 'mutation' but it is not proof, for without thorough factor analysis it is impossible to distinguish between 'mutations' and 'recombinations'. As in *Botrytis cinerea* such analysis is, as yet, not possible, it seems best merely to describe the new form as a non-reverting discontinuous variation; but, if one wished to classify it according to Baur's scheme there would seem no option logically to its inclusion in the class 'combinations', that is, the more inclusive group of subordinate logical rank.

The origin of the strains that are found in nature is an extremely interesting problem. It is usually considered that, as the numerous closely related strains differ from each other apparently in the same way as discontinuous variants in culture, they have arisen as discontinuous variants from an original ancestor, and it is usually implied that such variants are of the nature of 'mutations'. Apart from questions of monophyletism and polyphyletism involved in this argument (and I must confess that the weight of evidence seems to me to point both in general and in particular to polyphyletism), and apart from the possible methods of origin of new forms in fungi that I shall discuss later, the existence of sexuality either recently or more remotely in time may give a satisfactory basis for the origin and continued presence of fungal and bacterial strains. The rare occurrence of amphimixis or of chromosome or nuclear aberrations within the individual

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[21] Compare also F. Chodat (1926) on *Phoma alternariacearum* and Hanna (1926) on *Coprinus sterquilinus*.

(Bridges 1923), would give possibilities of the formation of many genotypes, and these different strains would be maintained by the asexual methods of reproduction so common in fungi. The process as I see it, may be similar to that suggested by Ostenfeld (1921) to explain the *Hieracia* or by Täckholm (1920, 1922) and Blackburn, and Heslop-Harrison (1921) to explain the roses. Attention may also be drawn to Turessen's (1922–1926) studies, which describe on a macroscopic scale for phanerogams a process that, I consider, may well happen on a microscopic scale in the fungi and perhaps the bacteria. The constancy of the fungal 'ecotype' or strain would depend upon the degree to which genetic selection by the environment had occurred and upon the possibilities of recomplication in hyphal growth.

2 *'Sectoring' or discontinuous variation in fungus cultures.* A further type of genetic research in fungi is the study of the discontinuous variations which, when the fungus is grown as a single colony on a plate, appear often as sectors but may show as raised or sunken spots, growths of distinctive color etc., secondary colonies or in other ways. 'Sectoring' has sometimes been treated as a phenomenon *sui generis* but this is probably not a correct point of view, the appearance being simply due to the fact that the variation arises at a point—one or more cells—in a mycelium which is radiating in a centrifugal manner on a surface. Detailed cytological studies of the point of origin of sectors are much to be desired. The phenomenon of sectoring is commonly compared with 'bud-sporting' of higher plants and, because this comparison seems to me essentially true for perhaps the great majority of these instances, I cannot forbear quoting Bateson's (1926) last words on this subject.

"A close study of the phenomenon of bud-sporting in plants may be expected to extend our understanding of the nature of the process of segregation and the principles which it obeys. I notice a disposition among the advocates of the chromosome theory in its cruder form to speak of all such sports as 'mutations'. Such an application of this term, for example, to the manifold sports which arise through the instability of any of the numerous arrangements of the components in a variegated plant is likely to introduce confusion. A branch of a new type may arise whenever one only of the components fortuitously comes to occupy a growing point, or by various rearrangements of the components, to mention only the simplest possibilities. Mutation is a term used in a great variety of connotations by various writers. To disentangle these, even if it were possible, is a task beyond my present purpose but in general I notice that the term is commonly employed to give an importance, even an evolutionary significance, to a change for which the common word variation is felt to be an insufficient description. To the consequences of rearrangement in a variegated plant such an expression is scarcely applicable and in so far as a bud-sport may be merely the emergence of a pre-existing component no question of mutation arises, even though the emergent member may have distinct genetical properties." Reference might also be made to Emerson (1922), Becker (1922), Noack (1925), Mol (1923, 1925) etc. On the other hand Schiemann (1912)

concludes that *Aspergillus niger* as commonly understood—and other authors for their own fungi—is an unstable or 'mutating group' comparable to *Oenothera* spp. In view of recent ideas on the *Oenothera* complex (Heribert Nilsson, 1922, Lotsy 1922, Davis 1926, etc.) this comparison may also hold much truth.

During the last few years I have had occasion to isolate a large number of fungi from soil and these have often been grown singly in plate culture. Many of these fungi have been in the laboratory for six years and have shown no sign of sectoring. In many other cases, however, one or more of a group of strains of diverse origin have shown sectoring whilst the collateral strains have remained constant. This is probably the explanation of my failure to confirm the results of Arcichowski (1908), Watermann (1912, 1913) and Schiemann (1912) in my repetition of their experiments (Briereley 1919, 1920). My work was all carried out on subcultures from two single spore strains and these strains of *Aspergillus niger* and *Penicillium italicum* proved constant genetically under all conditions. It is interesting to compare the ease and certainty with which Haenicke (1916) obtained variants,[22] with the rarity and difficulty of their production in Schiemann's (1912) researches, and their absence in my particular cultures. The outstanding fact in my own experience, and this, so far as I can glean, is in agreement with that of other mycologists who have paid much attention to pure cultural work, is the constancy of fungus strains and the 'reliability' of their cultural reactions. On the other hand, equally clear and definite is the genetic inconstancy of a minority of fungus strains, this inconstancy being in most cases apparently of a particulate or quantitative nature. The variants may give the appearance of a continuous change due to the difficulty of finding any well marked or quantitative distinguishing criterion in the structure of the fungus or in its cultural reactions. In isolation, however, the variants prove to be distinct entities which may revert sectorially or may give rise to further variants which, in turn appear to be discontinuous entities. The process is reminiscent in fact of Galton's polygon or rearrangement of atoms in molecular structure. The results of my own experience and a careful study of the data of many workers who have examined this type of variation, make it difficult for me to consider that this phenomenon occurs fortuitously and suggest markedly that this type (or types) of variation-process follows strictly causal laws expressed in or associated with a particulate mechanism of heredity.

In many of the fungi in which sectoring has been described there is the possibility, as Stevens (1922) has pointed out, of a 'heterozygotic condition', and this holds true for most, if not all, of the later records. Asexual reproduction for countless generations would not eliminate such genetic complexity (as Stevens 1922 apparently suggests) but merely perpetuate it. Now the evidence from other groups of plants seems to indicate that polyploidy, irregular nuclear divisions, chromosome aberrations, etc, which often result in somatic segregation and bud-sporting, are usually associated with apomictic types which originated

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[22] Dabei treten sie ausserordentlich häufig auf, gleich bei erstmaliger Anwendung der Gifte und zwar bei manchen Giften fast mit der Sicherheit physiologischer Versuche."

probably by hybridization (compare Winge 1917, Rosenberg 1917, Ernst 1918, Holmgren 1919, Täckholm 1920, 1922, Emerson 1922, Noack 1924, 1925; see also Wilson 1925, Sharp 1926, Bateson 1926). In the type of asexually reproducing but possibly heterozygous fungi in which 'sectoring' has most frequently been studied, somatic segregation by some such kind of nuclear re-organisation might give rise to sectors. Without in the least "suspecting the presence of the heterozygous condition as more or less universal throughout the fungi" (Brown 1926) I do think the suspicion is justified that it may not be absent in particular strains of certain fungi, possibly it is to some form of segregation in these heterozygous strains that we may look for the genetic explanation underlying some of the phenomena of sectoring. The fact that inconstant strains usually vary only in particular characters might, on this hypothesis, mean that they were heterozygous for only those characters, and this assumption would explain many of the difficulties connected with the incidence and distribution of inconstant characters in these strains.

The extreme difficulty of ensuring genetic purity even in Hymenomycetes is exemplified in the work of Vandendries (1925), Gilmore (1926), and Newton (1926); and in the Mucorineae by the work of Burgeff (1914, 1915) and Blakeslee (1920). In the Ascomycetes and Fungi Imperfecti the difficulties seem to me incalculably greater. In any case where there is the slightest justifiable doubt of the genetic purity of the organism giving the variants I must agree with Lotsy that there can be no question of classifying the variation in any higher category than that of *'combination'*. As a matter of fact, most Ascomycetous and imperfect fungi are, in our present state of knowledge, quite unsuitable for genetic work other than the testing of the frequency, direction, scope and stimulus of variation in the general sense, or the efficacy of selection within the clone. There is yet no method of analysing and resynthesising isolated components of these fungi by genetic criteria as can be done with certain Hymenomycetes, Smut fungi, Yeasts and to a lesser extent certain Zygomycetes, and, until such methods can be discovered, mycologists studying these forms are in the same position that chemists would occupy in a study of transmutation of elements if there were no methods of exact chemical analysis and synthesis.

3. *Mixochimaeras,* Under this heading I wish to suggest for discussion an issue which I recognise full well is controversial; some will say merely hypothetical. It is, however, a direct inference from the consideration of a mass of published data, and explains many data for which, at the present time, I know of no other equally good explanation.

Particularly during the last ten years an outstanding feature of mycological research has been the recognition of the genetic value of hyphal fusions in fungi, fusions which, in many cases, are correlated with the phemomena of heterothallism and sexuality. Further, it is well known that nearly all fungi when grown in culture show anastomoses between hyphae of the same colony, of the same strain or of related strains. In the examination during several years of many thousands of mixed platings of fungi from soil suspensions I have frequently observed

fusions not only between hyphae of different more or less closely related strains, but from time to time unmistakable fusions between hyphae of different species,[23] and of different genera. The coenocytic fusion-cell must, in such cases, contain a mixture of cytoplasm and nuclei (unless one component dies and of this there is no obvious sign) the complexity of which will depend upon the degree of kinship of the fungi whose hyphae anastomose. This type of fusion, taken in conjunction with the cytological structure, methods of wall formation and growth of fungi might, in certain cases and at more or less frequent or rare intervals, lead to hyphae of *mixochimaera* type. I have previously (Brierley 1920, 1922) used the term 'heterocaryotic', but as this has recently been misinterpreted as 'heterozygous' (Brown 1926), I have adopted the term 'mixochimaera' which was used by Burgeff (1914, 1915) for a mycelium derived by hyphal fusion and containing cytoplasm and nuclei of distinct types.

Such mixochimaeras have been experimentally synthesised by Burgeff (1914, 1915) and, in fact, this condition occurs to a greater or lesser degree in all the recent species or strain hybridizations in fungi.[24] I would suggest that it is by no means impossible in view of the characteristic methods of hyphal growth and direct conidial abstriction, that new strains or types of fungi might arise, some of which might be constant and others inconstant, according to the balance of nuclear and cytoplasmic elements in the cells of the mycelium (compare Burgeff 1914, 1915, on *Phycomyces nitens* and also Calkins 1926, on the results of conjugation in protozoa). If in such mixochimaeras, the components possessed different growth rates, as is suggested in Burgeff's 1915 cases, one might obtain an appearance of continuous variation under certain conditions or discontinuous variation under others, and the reverting or non-reverting qualities of a particular form would depend upon the degree to which the conditions had influenced the genetic balance. A form that had established an equilibrium might be thrown out of balance by some drastic treatment with chemicals, etc. (compare Schiemann 1912, Haenicke 1916 etc), or even by slight unrecognised changes in its immediate environment so that an apparently constant form might suddenly give the appearance of inconstancy (Leonian 1925; see however, Ermerson's 1922 warning). I would suggest that certain of the more astonishing, or even bizarre, results in the recorded data of variation in fungi become comparatively simple and obvious on this hypothesis.

A point to which I would direct attention here is the exceeding commonness of fusions beteen the germ tubes of fungus spores. In the yeasts, smut fungi[25] and Hymenomycetes the genetic value of such fusions is recognised, but in the Ascomycetes generally Phycomycetes and Fungi Imperfecti they are ignored, and yet mycological literature is full of indications that they may be of considerable genetic iuterest. To indicate a recent case only, and this could be replicated in

[23] Compare Kniep (1926).

[24] Compare for example, the interesting work of Müller (1924) on *Rhizoctonia solani* with the selective hyphal fusions described in this fungus by Matsumoto (1921).

[25] cf. Kniep's (1926) recent paper for striking examples.

many fungi, such observations as those of Dreschsler (1923) on *Hemlinthosporium* should certainly be followed up genetically.[26]

A further question that may be raised in this place is the almost entire absence of cytological information in relation to sectoring and other variation forms in fungi, or indeed of the vegetative cells of fungi in general (compare Kühner 1926). Haenicke (1916) found that in certain cases number of nuclei was corelated with distinct morphological variations. (Compare the work of Hegner 1920 on *Arcella*). To take this one point only, I have during the last few years had occasion to stain suspensions of spores of many soil fungi, such as species of *Penicillium, Aspergillus, Mucor, Fusarium, Monilia*, etc., and, it is by no means an infrequent thing, to find varying numbers of nuclei in spores. It may be that some simple explanation such as this underlies Schouten's (1918) interesting results with *Aspergillus Wentii*, or on the other hand, a more subtle form of segregation may be involved.

I have here only been able to indicate an hypothesis which I think is strongly suggested by the data of fungus variation. It is, of course, speculation, but it is at the same time direct inference from data, and it may have value in that it does fit a considerable number of data for which at present I see no other feasible explanation. It will naturally stand or fall as it meets the pragmatic test of fitness.

H. General Conclusions

If the lines of thought indicated briefly in the foregoing pages are followed out and one takes a broad and comprehensive view of the data of variation in bacteria and fungi certain generalisations emerge. The mass of data would seem to fall clearly into the two categories, '*modifications*' and '*combinations*' and many variations in the latter class may be explicable in terms of somatic segregation originating in one form or another of cytoplasmic or nuclear re-ordering. It may be that certain of these variations will ultimately be shown to be genetic alterations involving a qualitative change, comparable perhaps, to the 'point mutation' in *Drosophila*, but this proof can only result from experimental analysis in individuals of known purity of genetic constitution. In the absence at the present time of such methods of exact study in most forms of fungi and bacteria, and with the doubt in all cases arising from the possibility of initial genetic complexity due to the sources I have indicated, there is yet, in my opinion no justification for the introduction of Baur's third category of 'mutations'. I would say of many of the fungi what Davis (1926) has recently said of the Oenotheras "Finally there is the accumulated evidence from various viewpoints . . . . which throws doubt on the genetical purity of Lamarckiana and of most Oenotheras that have been carefully studied, and leads us to believe that the genus is chiefly an assemblage of impure species. Attempts to establish evidence for mutation from such material must expect keen scrutiny and criticism from geneticists."

The evidence seems to me to point clearly to the fact that the fundamental concepts of genetics may apply in general and in particular to the bacteria and

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[26] The recent observations of Zeller (1926) (see also Cayley 1921) on the macro-conidia of *Nectria* are also of the greatest interest from this point of view.

fungi; with, as in all other groups, local modifications due to the special structure and functioning which gives these groups their taxonomic status.

From time to time other points of view have been suggested in explanation of the data of variation in fungi and bacteria. Gurney-Dixon (1919) elaborated an enzymic theory which bears many resemblances to the views of Beijerinck (1912), and in different guises has been suggested by many other authors. Fick (1923), Durken (1922) and others have hypothesised a gradual summation of plasmatic progenes until permanent variations are attained and this is somewhat similar to Beijerinck's 'progenes' and 'submutations' or the 'premutations' and 'mutations' of De Vries (1924). Richet and Cardot (1919) modify the old De Vries idea of mutating periods alternating with periods of relative stability. Gorini (1922) attributes changes in characters to a kind of cumulative Darwinian selection of individual modifications. Adami (1918) and Bergstrand (1924) regard variations in a Lamarkian sense as due to direct impression of conditions, while Montemartini (1916) carries this still further and considers fixity of genotype entirely absent, strains, etc. being merely local temporary forms adapted to nutritive and other conditions. Felix (1922) regards changes as caused by gradual destruction and gradual formation of those portions of cell substance which bear the particular characters, and this is not unrelated to the Mnemic hypothesis which in various guises is held by many workers. Morishima (1921) thinks that new characters may only be developed if they are already latent in the organism and Toenniessen (1921) states that variations may be due to change in dominance of unit characters. McLean (1923) considers "mutation" as a kind of "collapse of the specific framework" and "acclimatisation" as a stretching of the organism's powers of response to their utmost limit by the avoidance of destructive shock—the original form dying out, the ecad becomes the species. Wolterech (1924) and many other authors consider that the more fundamental characters are carried in the cytoplasm and not in the nucleus, and this view resembles in many ways that of Harper (1918) on algal characters and the "karyo-genetic" and "organismal" characters of Gates (1920). Küster (1918, 1919) suggests that non-reverting changes are due to unequal nuclear division and reverting changes take origin in cytoplasmic causation.

The above views, and their many variants that have been put forward during the last fifteen years all accept the data of variation in fungi and bacteria at their "face value," but as I have tried to show, this is not a tenable position, in many cases the phenomena being obviously not objective data but percepts resolvable into simpler elements. Moreover, so far as I can understand these views, no single one fits the data so comprehensively or makes fewer assumptions than the one I have suggested which is simply the application of common genetic concepts, criteria, and terminology to these groups of organisms.

In conclusion, I should like to put forward a personal point of view. In the application of mycology in industry, in animal and plant pathology, or in the breeding of animals and plants for resistance or immunity to disease, it is of primary importance that we should know the scope, directions, frequency, and

conditions of variation in fungi and bacteria. To have value this work must be critical and therefore must be carried out by consecutive genetic analysis of pedigreed individuals and cultures. Such researches include the study, from both the physiological and morphological aspects, of sectoring and other forms of cellular segregation in fungi and bacteria, the testing of the efficacy of selection in pedigreed cultures, the investigation of life-cycles, stabilisation of growth-forms, and the potentialities of physiological gradience and cyclical developments. Further, it includes the study of the protoplasmic, nuclear, and cellular bases underlying these changes. These lines of investigation will I think give results of first-class practical value and immediate application, and, if genetic criteria are rigidly adhered to, will help to clarify the present confused issues in bacterial and fungal variation. This work, however, is all analytical and I am not sanguine that it will throw much light upon the fundamental bases of our subject. It is only when we can first analyse and then resynthesize that advances will be made in our philosophy. Mere unending analysis, which is what the greater part of mycological research amounts to, may brilliantly advance knowledge and immediate practice, but I do not think that it will add much to thought or, of itself, give birth to new principles. Some of the newer researches have shown the possibility of synthetic study of fungi and bacteria and it is this new key which is the most valuable gift of this work. Such genetic research in bacteria and fungi, as in all groups of organisms, demands specially chosen material, for many types of organisms are completely unsuitable for genetic study while others are peculiarly favorable. There are many indications that such groups occur in the bacteria. In the fungi many of the Hymenomycetes are out standing, but I am not sure that many Smut fungi and Yeasts and perhaps heterothallic Ascomycetes may not prove equally suitable. Certain of the larger Oomycetes may also have value. The Zygomycetes and many of the imperfect fungi with large multinucleate hyphae and conidia would seem to be peculiarly favorable for the study of "mixochimaera" phenomena. Any fungus which has distinctive characters and is large enough to manipulate, which can be easily and quickly grown in culture and reproduces freely, which shows heterothallism, or sexuality in which the two elements can be isolated or brought together by modern methods of "micrurgy" is potentially suitable material for genetic research.

Finally, I would plead for the adoption of a far wider and more comparative viewpoint in our mycological studies. It has recently been said that this is merely to speculate and reason by analogy, but to view the phenomena in their wider and more general biological setting and not to see them with myopic vision as sporadic and fortuitous happenings; to understand them as elements that are found to fit naturally into the pattern of a logical mosaic of genetic theory—this is not mere analogy and speculation. As it appears to me, it is the application of the comparative method which, by its fruitfulness in the past, has proved its fundamental value and, perhaps, in no field more strikingly than in genetics. Wilson's (1925) attitude in the study of Protista is, I think, equally valuable in our special field—"In practice however, the process in Protista offers many difficulties which often compel us to interpret the observed phenomena in a

measure deductively in the light of our knowledge of higher forms." A great amount of mycological research today is extremely parochial in outlook, it shows little knowledge of what is recorded in the literature of the subject and less appreciation of the wider implications of the facts derived from the immediate research or their relation to the data from similar researches in other groups of organisms or other fields of biology. I cannot help feeling that, unless we make some attempt to draw together our lines of research and correlate our facts and concepts, we shall be overwhelmed by a chaotic mass of meaningless data.

I recognize full well the theoretical—some will say merely speculative—nature of much that I have said, but I make no apology for this, for I believe with Wilson (1913) that "We have much to gain and nothing to lose by the use of explanatory hypotheses that are naturally suggested by the facts and help us to formulate them for analysis, so long as such hypotheses are not allowed to degenerate into dogmas accepted as an act of faith, but are only used as instruments for further observation and experiment." Personally I have found the point of view that I have put forward the most satisfactory in our field of mycological genetics, and, so far as I can see, it is the only one which covers all the data. It may have value in stimulating further research, but it is entirely tentative, and it will stand or fall by the pragmatic test of fitness to new data.

CONTRIBUTION A LA FLORE DES ENTOMO-
PHYTES DE L'UKRAINE[1]

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La glèbe noire et fertile d'Ukraine abonde en plantes mais les insectes nuisibles fourmillent de même et dans la destruction de ceux-ci, les entomophytes ne sont pas les derniers à jouer un rôle important. Favorisant la disparition de certaines espèces, par contre le développement d'autres, ils agissent comme facteur d'équilibre.

Tandis que les parasites animaux livrent aux insectes une lutte presque sur chaque point du territoire, eux, les entomophytes, parasites végétaux, n'opèrent dans leur oeuvre de stérilisation que localement, du centre d'un champ à sa périphérie (mobilité des premiers, sessilité des seconds).

Pour les avoir particulièrement étudiés, je tendrai dans cette communication, à décrire surtout les entomophytes du charançon des betteraves à sucre. Il s'agit d'une espèce de *géochton*, ou plutôt *d'entomophytogéochton*, par analogie avec le *planchton* mieux connu et objet de plus fréquentes recherches.

Parmi les bactéridies, c'est le *Pseudomonas ucrainicus* mihi qui m'a semblé le plus important et le plus caractéristique comme microbe pathogène au moins en ce qui concerne les larves du *Cleonus punctiventris* Germ. Je l'ai décrit dans le Bulletin de l'Académie des Sciences de Cracovie en 1904. Il se trouve dans les novales et disparaît des champs de vieille culture. C'est probablement un microbe forestier qui succombe dans les champs exposés au soleil. Néanmoins il est très virulent même dans les cultures artificielles à condition qu'on le renouvelle en contaminant de temps en temps un insecte quelconque et en ressemant de nouveau sur un milieu artificiel.

Tout comme le *Pseudomonas* la *Botrytis bassiana* Bals., les trois *Isaria, I. farinosa* Dicks, *I. fumosorosea* Wize, *I. smilanesis* Wize, les trois *Acremonium, A. Danyszii* Wize, *A. Cleoni* Wize, *A. soropsis* Wize, la *Pseudomortierella Cleoni* Matruchot et Wize, *Verticillium Oksanae* Matruchot et Wize, *Olpidiopsis ucrainica* Wize et *Strumella barbarufa* Wize et *S. parasitica* Sorokine (?) me semblent être des entomophytes forestiers qui ne peuvent subsister longtemps et en quantité remarquable dans les champs exposés au soleil.

Toutefois il existe trois entomophytes, *Oospora destructor* Delacr., *Sorosporella uvella*. Krass., et *Massospora Cleoni* Wize, qui font exception, étant mieux adaptés à la vie dans la terre des champs. Leur infection au sol augmente de la première culture des betteraves aux suivantes.

Oospora destructor Delacr., la "muscardine verte," détruit dans les champs de vieille culture jusqu'à cent pour cent de toutes les larves et chrysalides du *Cleonus*. C'est un champignon champêtre par excellence. Tandis que l'*Isaria* tend à former les conidies à la surface de la terre où le soleil les tue, l'*Oospora* forme des conidies dans le sol, sur l'enveloppe de l'insecte momifié, sur le parois de la

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terre du cocon et même entre les mottes de terre. La muscardine verte se laisse cultiver artificiellement en des nombreux milieux nutritifs et par ses spores elle contamine facilement toutes les espèces d'insectes. Les spores ou plutôt conidies, restent longtemps intactes dans la terre cultivée, du moins quatre ans, d'une culture de betteraves avec l'invasion du *Cleonus* jusqu'à l'autre. Les sclérotes du champignon de l'intérieur de l'insecte momifié se dissolvent partiellement en conidies, mais souvent ils succombent comme proie d'un parasite secondaire le *Gymnoascus umbrinus* déjà connu dans son rôle de parasite d'*Isaria*.

Sorosporella (*Tarichium*) *uvella*. Krass., la muscardine rouge, est un concurrent de l'*Oospora*, contaminant en même temps que l'*Oospora*, jusqu'à 60 pour cent de toutes les larves et chrysalides du charançon. Elle forme à l'intérieur de la larve ou de la chrysalide des azygospores (?) rouges, que l'on peut cultiver artificiellement en des milieux nutritifs. Mais, elle ne contamine pas les insectes, ni par ces cultures ni par ce qu'on trouve dans l'insecte. Peut-être a-t-elle besoin d'un hôte intermédiaire, peut-être possède-t-elle deux formes d'existence comme les Ustillaginées.

Une autre espèce de la muscardine rouge du *Cleonus* est la *Massospora Cleoni* Wize qui rappelle la *Massospora cicadina* Peck, bien connue en Amérique. Pendant que les azygospores (?) de *Sorosporella* ont une consistence pour ainsi dire sablonneuse, les zygospores (?) de *Massospora* ont celle du talcum. La couleur est rouge-orange, tandis que le rouge de *Sorosporella* est plus foncé. Les zygospores se forment du mycélium et l'on peut les étudier dans presque tous leurs stades. Chez la *Sorosporella* on n'observe que les azygospores à l'état naturel. Ce ne sont que les cultures artificielles qui donnent des cellules jeunes rappelant la levure des cellules que nous avons nommées azygospores. *Massospora Cleoni* est une muscardine rare, mais elle se trouve toujours en quantité considerable au même lieu, jusqu'en des vingtaines de larves et de chrysalides contaminées. Comme toutes les entomophtorées (?) elle ne peut être cultive artificiellement.

En dehors des entomophytes énumérés jusqu'à présent, j'ai encore aperçu en Ukraine la flachérie, surtout dans des chenilles de la *Saturnia spini*, le *Bacillus larvae* White, les *Empusa Aulicae* Reich, *E. Grylli* Nowak, *E. Muscae* Cohn et aussi la *Stigmatomyces Baeri* Peyr, l'épiphyte aussi beau qu'inoffensif.

On trouve l'*Empusa Muscae* très fréquemment dans la *Pegomyia conformis* Fall,—du printemps jusqu'à l'automne. On voit des vingtaines et des vingtaines de ces mouches mortes de l'horrible maladie et putréfiées, attachées aux tiges des plantes, sur le bord de la route et aux, lisiéres des champs.

Deux autres épiphytes la *Strumella parasitica* Sorok. et *Strumella barbarufa* Wize, déjà nommées ci-dessus, sont moins inoffensives que la dite *Stigmatomyces Baeri* et les autres Laboulbeniacées. Elles déterminent des tumeurs sur la peau de larves, la première sur les larves du *Polyphylla fullo* L., la seconde sur les larves et les chrysalides du *Cleonus*. Quelquefois la larve semble s'être affranchie de la maladie en muant de peau, mais dans la plupart des cas, surtout chez la *Strumella barbarufa* le sclérote du champignon pénètre à l'intérieur du corps de la larve ou de la chrysalide et cause aussi la mort de son hôte.

MYCOLOGICAL NOMENCLATURE[1]

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The primary question in connection with mycological nomenclature is, as I now see it: How can the greatest degree of uniformity and stability in the use of generic and specific names be attained in the shortest time? This is an important problem confronting systematists and seriously affecting all others who need to use the Latin binomial nomenclature.

There has been so much fruitless and impractical discussion of this subject in the past that many botanists hesitate to take part in it any longer. It certainly is a disgrace that such a comparatively trivial matter cannot be settled by general agreement and cease to occupy the time and energy which are so much needed for more profitable work on the numerous and important problems in mycology which confront us. Notwithstanding the disagreements of the past I still have hope that our consideration of this subject may lead to some improvement. In any case it is futile to discuss the subject unless there is some principle, purpose, or definition upon which we can agree. The essential purpose and function of nomenclature, as I understand it, is to provide a reasonably stable, convenient, uniform, and accurate means of designating various groups of living organisms. I am also assuming that Latin or Latinized binomial names are the most satisfactory for present purposes. Numerals or other symbols have been proposed, but do not appear to be satisfactory substitutes for binomials.

In contrast to the above statement of the function of nomenclature we may add that in our opinion it is not a primary or essential purpose of nomenclature to give credit to the discoverers of undescribed plants or to distinguished botanists, though this may be done where it does not interfere with the primary purposes of the names. Neither is it an essential part of nomenclature to give credit to the person who first applied a Latin name to a plant.

In connection with the priority principle it has been urged that there is an important ethical consideration involved in our use of names—that when we fail to find and adopt the oldest name for a plant we are doing an injustice to the one who first gave it a name. Such considerations I used to take seriously, but it is now evident that they are purely academic rather than ethical and are so far outweighed by the practical and scientific considerations involved as to be nearly or quite negligible. Moreover, the most ardent advocates of priority refuse to go back to Tournefort and Micheli, the real founders of genera, and give them the credit they deserve.

[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 18, 1926.

What is most needed is to secure such uniformity in the use of binomials that a citation of the author will not be necessary in order to make the application of the name perfectly clear and certain. I believe in giving full credit and honor to whom they are due, and especially to scientific workers who have never had proper recognition by the public at large. There is, however, little credit due to many who have named plants, especially where they have given names to poor, scanty, or worthless material, or published brief and inaccurate descriptions in more or less inaccessible works and the species are not represented by accessible type specimens. The time has come when in the interests of economy, efficiency, and the progress of science the investigator is justified in ignoring work which does not show a reasonable degree of scientific knowledge and accuracy. It is time that certain standards of work should be demanded in order to justify recognition.

If systematic mycology is to be regarded as a legitimate branch of the science of botany it must be pursued in a scientific spirit and according to the best scientific methods. It would seem evident that these questions of nomenclature should be discussed and determined not on the basis of personal preference or prejudice nor from national or racial standpoints, but with the sole purpose of determining what will best serve to advance botanical knowledge and its practical application. In the past the matter has been considered chiefly from the standpoint of the specialist in systematic botany, while the needs of specialists in other branches of botany, as well as those of amateur workers and economic botanists, have received little consideration.

If we agree that the aim of nomenclature should be to secure accuracy, uniformity, and stability in the use of names the next question is: How can this be accomplished? Stability and uniformity do not seem to have been very seriously considered by the earlier mycologists. Fries, Persoon, and others made new names in place of earlier ones because the earlier ones seemed inappropriate. They also changed names or adopted others without reference to priority or appropriateness. Appropriate names are preferable and should be selected if possible in naming undescribed species, but from the standpoint of stability and uniformity the change of inappropriate names already established causes far more harm than good. The inconvenience caused by such a procedure far exceeds any advantage gained. The same is true in cases of change made on account of priority of publication. In a previous paper[2] we have attempted to summarize the results of the attempt to apply the principle of priority to all binomials, using in every case the oldest name only. The results so far are very unsatisfactory and give little promise of securing for us within any reasonable time and with any reasonable amount of labor the uniformity and stability so much needed in mycology. The possibilities in the shifting of names of fungi are almost unlimited, if an attempt is to be made to put them on a priority basis. This combined with the difficulties and differences of opinion in regard to the early descriptions and specimens would probably lead to more constant and innumerable changes than would be produced by any other plan.

[2] Shear, C. L. The failure of the principle of priority to secure uniformity and stability in botanical nomenclature. Science, N. S. **60**: 254–258. 1924.

If credit to the describer of a species is to be considered important the honor should go to the one who has given the best description or illustration and is backed by the best specimens. This would probably cause less change than following the strict law of priority and would also eliminate at once many names now nearly or quite *nomina nuda*.

How then can we most quickly and most satisfactorily secure a reasonable amount of uniformity and stability in the names of fungi? My conclusion, after many years of study of the subject, is that this can be most quickly and easily accomplished by following general usage wherever practicable. The first objection to this plan usually is that it is too indefinite and uncertain for practical application. Of course there are many cases in which it would be difficult to decide what name to adopt. This I believe could be satisfactorily determined by a nomenclatorial committee of mycologists familiar with the different groups and in sympathy with this plan. The committee having chosen a name it should be generally adopted and not subject to further change. There is nothing new in this plan. It is simply a proposal to more or less indefinitely extend the list of *nomena conservanda* of the Vienna-Brussels code. It means the application of what our German colleagues call the "Bequemlichkeits-Motiv" in a broader and more general way. Instead of making this a minor feature in fixing names we would make it a major feature. It would be applied to all the large and important genera and species, especially those of economic importance. For small and unimportant genera and species, where to follow priority of publication would cause little inconvenience or change, that plan might be adopted.

In order to make the application of this plan clearer I may cite a few examples of generic and specific names which would be conserved and stabilized in this way. The genus *Agaricus*, which originally included nearly all the gill fungi, but which until recently has generally been applied at least to a group of species containing *A. campestris*, would be adopted instead of *Psalliota*, as used by some recent authors, and fixed by the nomenclatorial type *A. campestris*.

Polyporus would be definitely fixed to a group of species having the nomenclatorial type *P. brumalis*.

Hypoxylon would be used for species congeneric with the nomenclatorial type *H. coccineum*. If priority were followed the type of *Hypoxylon* would be the present *Xylaria polymorpha*. Such a change as this would certainly besome what confusing.

Xylaria would be fixed to a group of species with the nomenclatorial type *X. polymorpha*. On the basis of priority the species of *Xylaria* would have to be called *Valsa*, as this was the first application of the name *Valsa* by Scopoli. Think of calling all Xylarias *Valsa!*

A few such changes as this, in the fungi, would seem to be sufficient to condemn the general application of priority.

Valsa, according to priority, whether taken from Adanson in 1763 or Scopoli in 1772 would replace *Xylaria*. To preserve this name in its present use the type must be taken from Fries in 1849 and we should designate it *V. ceratophora*.

Puccinia would be conserved instead of *Dicaeoma* with the nomenclatorial type *P. graminis*.

Uromyces would be conserved instead of *Nigredo* and take the nomenclatorial type *U. appendiculatus.*

I trust these examples are sufficient to indicate how the proposed plan would be applied and also give some slight suggestion of the change and inconvenience which would be avoided by following it.

It would also seem rather evident that there can be no stability or uniformity in the use of names without some method of preventing the constant shifting now going on. The shifting of generic names from one group of species to another has been a frequent practice in mycology. It is perhaps most strikingly illustrated in the work of Saccardo. This shifting can be largely if not entirely remedied by adopting a nomenclatorial type for each genus and species, thus fixing the application of the name at one point at least. Then whatever changes in the limits of the genus or species are made on account of different generic and specific concepts the original name will still be fixed at one point.

It is said that too much stability in nomenclature may prevent or interfere with the advancement of taxonomy and that names must be changed in order to meet the requirements of increasing knowledge of plant relationships. This, however, need cause little change of names. New concepts of the limits of genera and species and their multiplication and renaming and shifting are not usually the result of advanced knowledge of genetical relationship, but are most frequently due to peculiar individual concepts and lack of a broad understanding of the real aim and purpose of taxonomy.

The nomenclature of fungi presents problems and difficulties not met with in flowering plants. The pleomorphism of most of the Ascomycetes and of many other groups, and our lack of knowledge of the life histories of most of them greatly complicate the problem. The difficulties connected with the positive identification of many species, owing to brief or faulty descriptions and lack of type or authentic specimens and the numerous synonyms which exist add to our nomenclatorial troubles. In spite of all these difficulties there appears to be one other important reason why we have not come to some agreement in this matter, that is, because we have not discriminated between the major and the minor problems, but have attempted to settle them all at once.

Whether we shall follow usage in all cases in which it is practicable and will prevent change of name, or whether we shall have strict priority whatever the results, seems to be of far greater importance than the question of duplicate binomials, or the capitalization of specific names, or the double citation of authorities, or the publication of Latin diagnoses or any of the other petty details which are insisted upon so strenuously. If we can agree upon the few really important matters the others can be settled later or be left to settle themselves.

The important things to settle first, as I see the problem, are the two questions, whether we shall follow strict priority or usage, with priority as a last resort, and whether we shall adopt the nomenclatorial type method of fixing generic and specific names or follow the present plan of shifting names from one group of individuals or species to another according to the whim of the taxonomist. If we cannot come to some agreement on these fundamental questions it would seem rather futile to discuss others.

BOTANICAL NOMENCLATURE IN RELATION TO MYCOLOGY[1]

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Possibly the best use of the time at my disposal will be to consider some of the more general rather than the more particular problems of mycological nomenclature.

There is apparently some confusion between what are the *principles* of nomenclature, the *laws* or *rules* which are formulated for applying these principles, and the *recommendations* made in order to avoid unnecessary complications in the future applications of the rules.

The principles of nomenclature are well stated in the International Rules as Article 4. "The essential points ('le principe essentiel') in nomenclature are: (1) to aim at fixity of names; (2) to avoid or to reject the use of forms and names which may cause error or ambiguity or throw science into confusion." Rules of nomenclature should be based on these principles and should be few in number and easy to understand. Mycologists must subscribe to the rules of Botanical Nomenclature. There is no possibility at present of International Rules of Biological Nomenclature—so far botanists do not agree amongst themselves and there are different sets of rules in zoology and in entomology. But it would be utter foolishness for mycologists to stray from the general botanical fold. What is the problem before us? In a few words it is that we wish to use a name which denotes an organism with certainty. All codes of rules of botanical nomenclature presumably aim at precising a name so that there can be no ambiguity. It is obvious that this cannot be effected satisfactorily if more than one code is in use, or if botanists pick and choose which rules they will follow, or if the rules are interpreted in different ways. Consequently it is a *sine qua non* now that there should be international rules. Nomenclature should not be treated either as a stunt or as a matter of national prestige. To regard it as anything other than from the standpoint of convenience and, moreover, as a subject for compromise, suggests a misunderstanding of the proper place of nomenclature in the science of botany.

As corollaries to this it is clear that it is useless to make rules which cannot be enforced. For example, how many mycologists trouble about the article in the International Rules which states that diagnoses are not valid unless in Latin. Even those of us who go so far as to put our own diagnoses in Latin do not hesitate for a moment to accept diagnoses in other languages that we can understand. Rules and recommendations should be clearly distinguished. For the general benefit workers should be recommended to do this or that; a rule should be regarded as a law, and if it is disregarded there should be a penalty.

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 18, 1926.

Assuming that we can agree on a set of rules, how can they be enforced? The only way appears to be through publication in normal channels. Societies, editors, and others should subscribe to an arrangement that all contributions in their periodicals follow the International Rules. At present a paper which followed no rules except those of the writer could be placed without very much difficulty, and obviously it is useless to attempt to control private publication. I am certain that all British botanical periodicals would agree to such an arrangement. If we cannot enforce rules we should restrict ourselves to recommendations.

The interpretation of rules requires some notice. In the International Rules it is laid down that the French text decides doubtful interpretations of English and German texts (Le texte francais . . . . fait foi au cas de doute sur l'interprétation des textes anglais et allemand).

The official translation of (Rule 39) Recommendation xviii *bis* reads: "When publishing names of new groups to indicate carefully the subdivision which is regarded as the type of the group: the typical genus in a family, the typical species in a genus, the typical variety or specimen in a species. This precaution will obviate difficulties of nomenclature if at some future time the group in question becomes broken up."

Hitchcock in his Descriptive Systematic Botany, 1925, p. 159, translates the Recommendation as, "When publishing names of new groups, one should indicate carefully the subdivision which one considers the nomenclatorial type of the group; the type genus of a family; the type species of a genus; the type variety or type specimen of a species. This precaution will avoid the nomenclatorial difficulties when in the future the group is to be divided." Is it not obvious that here we have two entirely different interpretations? If "typical" and "type" are to be interchangeable, what are we to expect when we get to details? Bluntly, nothing more than we have already had will mix nomenclature and taxonomy as in synonyms, and any one with the necessary mental equipment can use that name he pleases with full legal support. Dr. Shear has suggested that a standardized list of fungous names on the basis of usage, similar to that adopted by American Horticulturists, would do away with most if not all of our difficulties. This at first sight appears to offer a solution, and probably most of us have at one time or another thought of a similar authoritative list. But nomenclature is only the handmaiden of taxonomy, and cannot remain stationary. Some name changes are inevitable; our aim should be to prevent wanton name changing which bears no relation to advancing knowledge. Mycology is making rapid progress in many directions and we as mycologists are not so much concerned with the past as with the present and the future. We must attempt so to gain ideas from our predecessors and our contemporaries that we erect a system capable of fulfilling future needs, and which does not act as a drag in any way on future development. A standardized list of names would not survive intact an issue of any mycological periodical. We might very well extend the "principle" of *nomina conservanda* to certain species but to apply it indiscriminately to all species would lead us into taxonomic stagnation.

Let us be quite clear as to that with which we are dealing. On the one hand we have fungi as living organisms; on the other, names, descriptions, figures, and herbarium specimens. I have discussed this in another place[2] and have attempted to distinguish between what may be termed natural species and taxonomic species. Taxonomy postulates the existence of natural species and attempts to diagnose them. Whatever the state of affairs in nature, it is obvious that the species of description vary greatly.

Adopting the type-method, the only thing that we can be certain about is that the name, description, etc. refer to an individual specimen. The more we precise a name, the more we restrict it. This is really what the objectors to the type method have in mind where they talk about general description. It is even more than they seem to have realized. If we have a type specimen of a species, and a type species of a genus, and, as some have suggested, a higher genus of a family, then are all based upon a type specimen, or its substitute? The International Rules, as we have seen, may be considered to have recommended the method and British and overseas botanists are agreed (by a majority vote at the Imperial Botanical Conference 1924) that the type method should be adopted, and this on the grounds that it enables the precising of names. This precision tends towards nomenclature stability but has nothing to do with taxonomic stability. According to the taxonomic treatment adopted, it is quite conceivable that a fungus may have more than one valid name.

A word or two seems called for concerning diagnosis. We do not often remain satisfied with an original description, but chop and change it in an endeavor to make it fit realities, whatever these may be. When we use a name we ought to have a special significance in mind. Disregarding misidentification, we mean that a fungus to which we give the name agrees in all respects with a certain diagnosis. We are usually very careless regarding the matter and frequently do not mention whether the original diagnosis has been consulted or one a hundred years later. Descriptions alter as knowledge increases. Can we expect, therefore, a hard and fast nomenclature such as a list of standardized names appears to be? Being convinced of the necessity of continued changes in nomenclature, due to the development of no taxonomic ideas, I feel that our best plan is to formulate rules which take this relation into account. This brings me to two suggestions.

(1) It is obvious that rules cannot be made once for all. We need some sort of finality about them, but new problems arise which require special treatment. International law offers many interesting analogies. If we can agree about a code of laws of nomenclature we ought not then to make indiscriminate additions. It is not until efforts are made to apply rules directly that real difficulties are encountered. To prevent the rushing through of rules I would suggest that an alteration in or addition to the rules should be brought forward at an international congress and that one or more botanists should be deputed to report before the next Congress the results which would follow these changes, and then a decision taken after full opportunity of studying them has been given. We can all cite examples of a casual statement being accepted at a Congress and leading

[2] Presidential address, Trans. Brit. Myc. Soc. 11:25-45. 1926.

to undesirable results. For example, would the different starting points for the nomenclature of fungi have been adopted at Brussels by 130 votes to 4 if there had been proper consideration of the matter?

(2) This concerns the interpretation of rules. Usually in connection with different rules examples are given which are regarded as illustrating the application of the rule. This method logically leads to what is known as "case law." We already have suggestions of the growing up of this. There would be no objections to it if nomenclature were an end in itself. In a few years we should have a whole mass of cases which would require specialists for their proper understanding and the arrival at a decision concerning a correct name might resemble the proceedings in a court of justice. To obviate this danger would it not be better to leave the interpretation of doubtful cases in the hands of our International Committee. Zoologists have, I believe, adopted this method with satisfactory results. I will not venture to suggest the men for this committee nor the best way in which they might accomplish their duties.

So far my remarks have been general to botany. Turning now to mycology in particular we immediately meet with difficulties in applying the type method. What are we to do with saprophytic hyphomycetes or with species which are only known in culture? These are now described with a mass of details which cannot possibly be made out in dried specimens—and cultures are unsafe. I do not bring forward any proposals because I am not certain that better ones would not be forthcoming if we considered the difficulties thoroughly and submitted these in the form of a questionnaire to working mycologists.

I imagine that it will not be in our time that finality will be reached in deciding what a species is. It may be said that this problem is not confined to mycology or even to botany. A mycologist, however, might be forgiven for imagining that mycology has more than its fair share of the difficulties. Much effort has been expended in the attempt to define a species. Lotsy in his *Evolution by means of hybridization* even puts forward the opinion that those who describe species ought to define what a species is, no matter whether the task is considered finished where the description has been made, or whether it is intended to make use of the described species to build up a more or less elaborate system. The most recent attempts to define a species is, I think, that of our colleague, Mr. C. Tete Regan, in his Presidential Address to Section D (Zoology) at the British Association last year. "A species is a community, or a number of related communities, where distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name." A *community* is defined as "a number of similar individuals that live together and breed together;" a *"competent systematist"* is not further defined.

Now it is self-evident that the suggestion that every systematist must concoct some sort of definition of what he means by species is mere essay-writing. However, it is not perhaps too much to hope that mycologists might come to some decision as to what they mean by a species of description, that is, a taxonomic species: in other words, what rank is to be given to true species, to be referred to by a binomial? To some it might appear a little late in the day to raise this

point but a glance through most modern mycological periodicals shows that fungi referred to in exactly the same manner are not necessarily of the same rank. This is both illogical and inconvenient. We may decide to define a species on purely morphological grounds and still have our differences concerning how much or how little constitutes specific difference taxonomically, and how far other matters than morphology might enter into diagnosis. None of this will make any of our binomial problems easier to solve, but we ought to be able to agree about what names should seem within the limits of personal idiosyncrasy.

Another difficulty in taxonomic mycology concerns the Fungi Imperfecti. A species here, although usually spoken of and treated as equivalent to a species in which we know the perfect stage, is really something different. We should speak of them therefore under a different name. The binomial of a completely known species should include its conidial form or forms. Wherever only conidial forms are known, these might be called form-genera and form-species. Many discussing species in fungi appear to have overlooked this distinction and consequently they have landed in taxonomic error.

Another matter which ought to be considered is the best way of precising diagnoses drawn up from cultures. Every mycologist knows that it is sometimes advisable or may even be necessary to describe fungi grown on media. It is common knowledge, moreover, that morphological and other differences are to be seen when different media are used. Bacteriologists who, on account of the small size of the organisms with which they deal, are unable to lay much stress on morphology have prepared several charts for descriptive purposes; the most modern of these is that of the Society of American Bacteriologists. No similar chart has been prepared so far for fungi, but French mycologists have had the matter in mind. Lutz and Guigner read a paper at the Paris Congress in 1900 dealing with Mucedineae and yeasts. In it they called attention to the recent bacteriological scheme of Grimbert, and they considered the suitability of a similar scheme for moulds and yeasts. They prepared Rankin's solution as a standard medium and gave details of fifteen modifications. Some years later Margine in his work on *Aspergillus* was of the opinion that the diagnosis of species drawn up from cultures should be established as far as possible at the optimum of growth and accompanied by temperature data and amplitudes of variation according to conditions of the medium. Though he mentioned the desirability of considering the subject at the Brussels Congress he apparently did not bring it forward. Below the rank of species the International Rules list sub-species, variety, subvariety, form, special form, individual. This is a series which requires very searching consideration. Is it now of much use in mycology? It is obvious that "forms specials" was interpolated in a series already doing duty for flowering plants, on the assumption that it was of necessity suitable for other plants. It is in this infraspecific zone that mycologists should concentrate at present. What rank is to be assigned to the different categories which are now the product of every research, and what names are to be used for them? How far are medium and host plant to enter into the definitions? A certain amount of clarity can be attained by realizing that a host plant in many instances acts as a selective medium. Further, we have the question of biometric methods of

differentiation. A rough division for easier discussion may be taken as variety, microspecies, physiological race, strain, and saltant.

When we consider physiological races (or whatever they are best called) we apparently have two kinds, one in which morphological differences may be recognized and one in which they do not occur. Strains or pure lines may be few and well marked or, on the other hand, so numerous as to be indistinguishable, for all practical purposes, from the individual, in the hierarchy of the International Rules. Saltants may remain fixed or may revert when subjected to growth on different media. What is a practical solution of the difficulty? What is the taxonomic convenience? If these different categories are definable, their occurrence must be recognized in taxonomy and nomenclature. We are not in the position of horticulturists who scrap what is not marketable and invest a form which suggests possibilities of profit with a name that has less of principle in its origin than that of a race-horse. In mycology the pressure comes mainly from phytopathologists. Here an investigator is often surprised to find that systematic mycology appears to lag behind. He fails to realize that it is frequently owing to the fact that he is himself pressing ahead. His results become part of the general mass of taxonomic mycology. The problem of taxonomy is to fit these results into schemes of classification and it is one that, with the advance of the precise knowledge necessary in studying disease-producing organisms, needs to be freed by systematists. We must soon decide what ranks are to be recognized and what method of nomenclature is to be used. Obviously we cannot decide here and now. Another point, where does the type method end? Does it stay there, or get beyond morphological difference, or not?

Many workers describing some form or other which they regard as perfectly distinct call it, say, "Strain No. 1" or may be "Form A." This in no way simplifies matters. If we wish to refer to this we get a name like *Mucor racemosus*, Popopki's strain No. 1, and as investigations proceed we have discussions whether this is the same as *Trichothecium roseum*, Leggit's Form L. If any organism is sufficiently noteworthy to be distinguished, it should receive a name. I am quite aware that this may result in a string of names which will rival those of a Welsh village, or of our Prince of Wales. So long as we restrict the use of a binary name to what we define as species we cannot go far wrong. The binomial system in some ways suggests rather a pious fraud. The name without the authority frequently means nothing; the authority without the emendation is often misleading; precision is obtained only by giving the date sometimes with the place of publication in addition.

In this short contribution I have not proposed solutions of problems, but have attempted so to put them forward that our special mycological difficulties might be recognized. They should not be rendered more difficult through the lack of a suitable nomenclature capable of expansion.

Our most urgent need in mycology is the election of a small International Committee which should consider the whole subject of mycological nomenclature. One or more of its members should be members of the standing International Committee for Botanical Nomenclature proposed previously, for it is only by the closest co-operation that we can formulate workable rules.

BOTANICAL NOMENCLATURE[1]

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It is highly desirable that the rules of nomenclature should apply uniformly to all classes of plants, so far as feasible. When for some special reason a rule needs to be set aside or modified, a resort to *nomina conservanda* would appear more desirable unless the number of names involved is very large. In the case of the Uredinales there seems to be no sufficient reason why any exception should be made to rules based primarily on those for flowering plants, that is, to the general rules of botanical nomenclature.

In both the American and International rules the fungi have been given only secondary consideration. In the several forms of the American rules they are understood to be included, but in the International rules they are singled out together with other groups of the lower plants for separate treatment in certain regards. The rusts are specifically restricted in two ways: (1) the starting point for nomenclature, and (2) the validity of names.

The International rules state that the starting point for the Uredinales, Ustilaginales, and Gasteromycetes begins with Persoon's "Synopsis Fungorum" of 1801. As to the Uredinales, this restriction appears to be nullified by the general principle on which all the rules are presumably founded, namely, that they "should neither be arbitrary nor imposed by authority." It must be that those who voted for this restriction were uninformed about the nomenclatorial history of the rusts. Did they know that only three genera, *Puccinia, Aecidium* and *Uredo*, had been established before 1801, and that only about a dozen species had been assigned to them, all of which appeared in Persoon's "Synopsis," practically without change? There would be no difference in the application of these names, whether the starting point chosen is 1753 or 1801. In view of these facts it seems that the exception made for the nomenclatorial starting point for the Uredinales is not required, whatever may be true for the Ustilaginales and Gasteromycetes, for which the writer, for lack of sufficient accurate knowledge, does not choose to speak.

As to the second restriction, the International rules state that among pleomorphic fungi only those generic and specific names are valid which are applied "to the state containing the form which it has been agreed to call the perfect form." They further specify that for the Uredinales this "perfect state is that which ends in the teleutospore or its equivalent." The writer is curious to know what those who framed this exception had in mind by an "equivalent" of the

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 18, 1926.

teleutospore, and also who are the persons included in the coterie indicated by the phrase "it has been agreed."

In the taxonomic history of the rusts it has occurred many times that what was named and described as an *Aecidium* or *Uredo* has proved upon later and more careful examination to be really the teleutosporic condition, and quite as often the spores that were described as teleutospores have turned out to be uredospores. This lack of discernment and correct interpretation occurred among the earlier taxonomists, as would naturally be expected, but just as frequently it has occurred and still does occur among the most prominent of present day systematists. The application of the rule in such cases would seem somewhat puzzling, but more than that, it should arouse the suspicion that possibly in many cases the so-called "perfect state" is not readily distinguished from the other states. As a matter of general information it may be well to set forth explicitly that so far as the gross appearance of the sorus or of its constituents is concerned, there is no set of characters by which the "state which ends in the teleutospore" can be determined. Aecia, uredinia and telia may have the same general structure, and their spores may closely resemble one another. The fundamental distinctions lie in large part with other characters.

If the rule was framed to simplify and stabilize the use of names among the rusts, it is a failure, according to the writer's taxonomic experience of nearly half a century. It is noticeable that the most conscientious supporters of the rule not infrequently transgress, presumably unintentionally, but nevertheless consistently in the interests of good practice. It may be surmised that the rule reflects an impression that the situation regarding the *fungi imperfecti* among the Ascomycetes is paralleled among the Uredinales. This is a persistent, but erroneous, notion. Whatever may be expedient for the taxonomic treatment of the Ascomycetes should not be permitted to be carried over or influence that of the Uredinales. The writer believes that there are no sufficient grounds to restrict the application of names among the rusts beyond those imposed by the general rules of botanical nomenclature.

As the purpose of rules for nomenclature is to secure uniformity and stability in the application of names, in so far as that is possible, and to have such names acceptable to taxonomists especially interested in the various groups, some means should be devised to permit the expression of opinion before any arbitrary exceptions to general rules become binding. The establishment of a list of *nomina conservanda*, which is undoubtedly a necessity, should be handled in the same way. Revision from time to time, both of the rules and of the list of conserved names, will undoubtedly be required as botanical knowledge increases. These matters could well be placed in the hands of a permanent validating committee empowered to investigate questions brought before them. After the publication of their results and a sufficient interval had elapsed to permit others to reply, their decision could be accepted as binding. In some such way the rules of nomenclature could be made a part of the advancement of botanical knowledge.

MYCOLOGICAL NOMENCLATURE[1]

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What is it we are trying to find out by a discussion of nomenclature, whether applied to fungi or to other plants? In seeking for an answer to one phase of this question, I find myself coming to the conclusion that in the minds of many taxonomists, it seems to consist of ideas to be obtained by looking backwards. May I therefore offer some remarks from the point of view of looking into the future; of facing the situation that has developed in the past and that is beginning to spell chaos in our nomenclatorial practices of the present. Does the situation lead us into the halls of legislation? Must we have new rules or can we revise the old?

Just what do we assume when we make laws to direct the *naming of plants*, and, what seems to be a much more important issue, *the re-naming of plants*? Whether a group of mycologists of the past have agreed what should be law, or whether we, today, were to agree on legislation, or even if, at some future time, all those concerned shall agree unanimously to a set of so-called laws, we or they would indeed be careless of the lessons to be learned from all history if we made ourselves believe that such laws will be permanent.

In another generation a new group of mycologists and pathologists will have appeared. New scientific facts beyond our present comprehension will have been discovered; new problems of nomenclature will have to be met, and it is not at all impossible to conceive of a state of knowledge about fungi, as well as about other plants, which will require an entirely new classification and therefore new nomenclatorial regulations. In such a future system even such uniformity as exists at present may be entirely wiped out and with it will go the carefully cherished rules of today. If for example, we act today on assumptions that are set up merely to safeguard our personal connections with the naming or re-naming of plants, we may be sure to wake up in the long hereafter, during our next reincarnation, say, and find our simple egoism swept away with the years.

It has always seemed to me that certain men, who have loved to sneer at the use of the authority names after plant binomials, even if their conclusions seemed impracticable and their arguments not always consistent,—that these critics, nevertheless, have pointed out a very present factor in the egotistical makeup of human beings, botanists not excepted. This form of trying to become immortal is only one of several forms in which the botanist has shown a narrowness of viewpoint and a lack of understanding of the problems of the present as they bear

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 18, 1926 .

on those of the future. We pride ourselves on the enormous and magnificent advances which have been made in the knowledge of fungi, especially in this immense American area within the life time of some of us; and I think we are justified in that pride. Yet any successful effort of ours, to bring this vast amount of knowledge under lock and key, in even the smallest part, so that the generations to come will either be hampered in making the same rapid advance, or will be compelled, in self defense, to overthrow it completely, would be a sad commentary on the stupidity of our generation of mycologists.

The *unqualified* application of the *idea of priority* is an example of what I mean, when I say that whatever legislation is enacted should have due regard for the mycologists of the future. Paper after paper could be quoted to confirm the statement that even in these days when the synonyms of a species are relatively few as compared with what they will be one hundred years from now, investigators are compelled to spend as much, or more, of their valuable time in following up the oldest names for their fungi than was required in the search after new biological truth. And this is not all. At the present rate of increase of publications and the accompanying rise of the price of paper, the continued output of such historical data is bound to reduce the general opportunity for publication of more important researches. To my mind, taxonomy is the foundation for most other botanical scientific research, and names should be as stable as possible in order that it may serve the other phases of plant study efficiently. Complete stability, it must be obvious to any one, can not be attained. Such a hope is merely the will-o-the-wisp calling us to the swamp of unattainment. Furthermore, stability of that sort would mean a stand-still, and therefore a failure of taxonomy to meet the progress of its sister studies like genetics, ecology, physiology, and so forth, of utter failure to play its part in the solution of future problems in the whole science of botany and its ramifications.

The cry has gone forth that the younger generation of botanists are no longer interested in taxonomy, and a remedy is sought. It has occurred to me frequently, that one, if not the chief reason, for this attitude among prospective professional botanical students, has been due to the general expressions of dissatisfaction with the instability of plant names, expressions more often coming from those botanists who do no work in the taxonomic field. In searching for the cause of such instability, which has become more and more irksome during my botanical lifetime, I can not find a cause I consider more serious than the now widespread application, without qualification, of this idea of priority.

Let me correct, at this point, any misconception as to the intent of my attitude. To those who think my statements too strong, and to those who are so constituted that research in the dusty remnants of ancient collections seems an attractive study and contains possibilities of valuable knowledge needed by the human race in its thirst for hidden or forgotten things, I would say I am not implying that these men are not as truly investigators in their chosen field as are any other historians; but I can not conceive that it is essential to modern taxonomy that their findings should be incorporated into the live machinery

of the modern world. The practical social worker in our cities is not compelled to follow as his daily schedule an obedience to regulations which the ethnologist has unearthed in his study of ancient peoples.

Nor do I feel so intensely on this matter of priority that it hurts my personal pride to publish names of fungi according to the established rules of any particular publication. But I am, nevertheless, always hoping that as time goes by more taxonomists will arise who can think in terms of the present and of the future, and who will help build our taxonomic house with modern timbers, rather than seek to employ the worm-eaten relics of ancient days.

Any other rules and regulations, past and present, are, it seems to me, of secondary importance. Qualification for each group of plants, according as the situation requires for each group, seems to me the only method that will bring approximate concordance in the future.

Of the other regulations, I will refer only to a few. There is the rule requiring a Latin description of new species. Although I had excellent collegiate training in Latin and Greek, nevertheless, since this is becoming more and more unusual in the education of American scientific students, especially those turning to the plant sciences, I consider that this rule is unwise and uncalled for when applied to our present and future American conditions. A central bureau of expert translators would be an easy solution. Local Latin scholars, and it is hoped that we shall always have them with us, can furnish central publications like Saccardo's "Sylloge," with translations on request from an author; in this way the ludicrous repetition of a description on the same page, such as appear in our American publications, will be done away with, and the space be made available for more essential matters.

Another regulation has to do with the matter of types, especially the type-specimen. A type-specimen is admittedly most desirable. It is a pity that there are those who think laws will solve all difficulties in this life, scientific and human. It is a pity that a committee of such persons is unable to proceed—let us say—in a retroactive manner, calling the old mycologists from their graves and making them provide a good type-specimen before recrossing the Styx. In the large group of fungi, the Agaricaceae, we rarely find types of any consequence in connection with the classic works of Persoon, Fries, Quelét, and others before them. Figures occur in abundance. These are collected in volumes and called "Icones," and to the moderns there is a thrill in that word. One of the intellectual pastimes of some mycologists during the last hundred years, has been to pass judgment on the identity of these figures.

Unfortunately one can obtain very little accurate knowledge of certain structures from these illustrations. All one can get is a conception! Here again the future demands consideration. Are we to pass on to other generations the unending task of passing judgment on pictures until they crumble into dust? Meanwhile, in Europe, where the types have been lacking, eminent students of the Agarics have attacked the thankless job of trying to put such species on a more clear-cut footing. They have patiently compared the illustrations and the descriptions of the old masters, like Fries, Persoon, and Quelét; they

have sought for and found such fungi in the fields and forests today, and have then passed judgment on their identity. Common sense, it seems to me, bids us to accept this judgment. But, says the doubting Thomas, how do we know that they had the correct species? The good Lord deliver us! How are the rest of us to know, except through our own conceit that these men are in error? My attitude is that of the highest regard for those European mycologists who have done us, far away in America, these invaluable services. A proper recognition of their efforts to establish a new starting point for the European members of the Agaricaceae, would, it seems to me, require recognition of it. Hence it has been my practice to write the name of the older author, say Fries or Persoon or Quelét, followed by the name of the man who gave us a dependable set of microscopic, as well as macroscopic data.[2] What do nomenclatorial rules do in such a case? Frequently they bind us hand and foot.

These and other considerations lead to the conclusion that in the Agaricaceae the unqualified law of priority is a dismal failure. That we can not even apply the rule to enforce reference to the "type specimen." For there is no type specimen in existence. Decidedly, all we can possibly have is a *type conception*, which lends itself to stability in the manner I have indicated, if we follow the dictum of common sense. This situation occurs also in numerous cases in many other groups of fungi.

I have only touched on a few of the problems troubling the mycologist, since others will be better qualified than I to tell us what has brought on the present impasse and to suggest a remedy.

For the present I prefer the middle road, the main trunk highway, which I believe is traveled by the most botanists. I believe in the proposition that when there are thousands of many-sized and many-shaped pegs, they can not possibly all fit snugly into the same hole. I would apply the historic doctrine of common sense, and leave out of account the personal and mercenary, and finally I would fit my nomenclature, first and last, with or without favor, as each case demands, to the everlasting truth in so far as I can discover it in the plant world about me.

[2] An example of this idea will appear as follows: *Cortinarius uraceus* Fr.—Ricken.

STUDIES ON RHIZOCTONIA CROCORUM (PERS.) DC. AND HELICOBASIDIUM PURPUREUM (TUL.) PAT.[1]

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ABSTRACT

The fungus *Rhizoctonia Crocorum* (Pers.) DC. has long been known, but in the sterile state only, as the cause of the violet root rot disease of various cultivated crops. Affected plants are characterised by the presence of a violet mycelial felt on the main root, from which are developed small sucker-like organs variously known as microsclerotia, or better as infection cushions or "corps miliaires."

From time to time there have been diverse speculations as to the nature of the perfect stage of this species of *Rhizoctonia*, based usually on observed cases of association, but hitherto no proof has been forthcoming of the connection of any of these forms. A complete summary of the literature on the subject was given by Duggar ('15).

In 1922 the authors were led to consider a new possibility, namely that the fungus described by Patouillard as *Helicobasidium purpureum* might prove to be the long-sought-for fruiting stage of the *Rhizoctonia*. The hypothesis was based on the close resemblance to *Helicobasidium* of a sterile felt found on a stem of black currant and on the subsequent discovery that the plant in question bore the infection cushions of *Rhizoctonia* on its roots.

Comparison of the mycelia of *Helicobasidium* and *Rhizoctonia* showed that the vegetative hyphae of the two fungi are similar in color, size, septation, and mode of branching. The authors therefore determined to test their hypotheses, if possible, by means of pure cultures and inoculations.

The successful isolation of *Rhizoctonia Crocorum* from clover has already been recorded by Buddin and Wakefield ('24). By the methods described in that paper the authors have since isolated undoubted *Rhizoctonia Crocorum* from potato, sugar beet, mangold, and possibly from *Urtica dioica*, though the latter strain has not as yet given any infections.

Helicobasidium purpureum, at the time when the work was begun, had only once been recorded in England. By a fortunate coincidence, however, it was found by Mr. W. M. Ware in the spring of 1923 associated with violet root rot disease of red clover. In 1925 and 1926 the authors were able to in-

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 19, 1926. (See Trans. British Mycol. Soc. 12: 116–140. 1927; Ibid. 14: 97–99. 1929.)

vestigate two other cases of the occurrence of this fungus. In one case, *Helico-basidium* was found growing over the roots of an ash tree, and at the bases of stems of the surrounding vegetation, chiefly *Mercurialis perennis*. On examination it was found that the roots and underground stems of the *Mercurialis* showed typical root rot with infection cushions of *Rhizoctonia Crocorum*. The second case occurred in a distinct locality, and there the *Helicobasidium* was associated with *Rhizoctonia* root rot on the roots and stolons of *Urtica dioica*. Thus *Helicobasidium purpureum* has been found in three widely separated localities and on three different host plants in close association with root rot having the characters of attack by *Rhizoctonia Crocorum*.

In the attempt to grow *Helicobasidium* in pure culture from spores, great difficulty was experienced at first owing to the peculiar germination and slow growth of the fungus, and the lack of experience as to suitable media. While the spores germinate readily in the presence of moisture, the further development of the germ-tube is dependent on conditions not altogether understood. Even on the most favorable media found, such as malt extract agar or malt-meat-extract agar, isolated spores usually produce a long unbranched hypha which becomes empty behind and has only a small amount of living cytoplasm at the tip. Such spores frequently die out without establishing colonies. Where many spores are sown together, however, growth is stronger; for this reason all the first cultures were started from mass spore deposits. More recently single spore cultures have been obtained, and the earlier noted cultural characters checked.

Spore cultures of *Helicobasidium* vary in appearance to a remarkable extent. Some strains assume from the beginning the reddish-brown color which is found in most cultures of *Rhizoctonia*. The majority, however, form at first a pale pinkish buff aerial mycelium, from which there may arise later purplish sclerotium-like masses. Such cultures produce a conidial form which agrees morphologically with the genus *Tuberculina*. The conidia are subglobose to ovate, 10–16μ in diameter or $10 - 18 \times 9 - 15\mu$, two-nucleate, and their germination is similar to that of the basidiospores. Similar conidia have been produced in cultures of *Rhizoctonia* isolated from infection cushions of roots of *Urtica dioica*, and in cultures of another strain of *Rhizoctonia* isolated from mangold.

From such conidia-bearing strains of *Helicobasidium* there sometimes arise in subcultures, particularly in those taken from the above mentioned violet sclerotium-like masses, forms which acquire the reddish or purplish-brown color which is characteristic of *Rhizoctonia*, and which remain always sterile. Similar sterile brownish cultures have been obtained from single-spore cultures of the conidia.

With certain of such dark-colored strains, derived from some of the original mass spore deposits, successful inoculations have been carried out. Carrots and miscellaneous clovers have been grown in sterilised soil, the soil being inoculated from pure cultures of the *Helicobasidium*. In all cases adequate controls were used. Eight such experiments, carried out with three strains

of the fungus, have given positive results, root rot with the characteristic infection cushions being produced.

At the same time there have been very many negative results, and none of the strains isolated from material associated with *Urtica* has as yet given positive results. This material is the only one from which single-spore cultures have been obtained, hence it has not yet been possible to produce root-rot with undoubted single-spore cultures. At the same time the *Rhizoctonia* isolated from *Urtica* has also given negative results, so that it is possible that that strain is not pathogenic to the host-plants used for experiment.

Known infective strains of *Rhizoctonia* sometimes fail to give results, and it is obvious that more information is required as to the conditions of infection by this fungus.

There is some indication from the authors' results that cultures kept for a long period in vitro lose their virulence. There is also some evidence that the conidia-bearing strains of both *Helicobasidium* and *Rhizoctonia* are less virulent than the sterile strains.

It seems possible that the fungus is in a plastic state, and that its pathogenicity, as well as macroscopic appearance, may be subject to saltation.

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During recent years the work of various investigators on the so-called asymbiotic germination of orchid seeds has aroused considerable interest. I had hoped to be able to place before you comparative results of symbiotic and asymbiotic germination, but as this is not possible I will take the opportunity of giving some of the evidence for my belief in the "so-called symbiotic theory of germination."

The general outline of the mycorrhiza problem as it concerns orchids is well known and consequently the barest summary will suffice here. Orchid plants, growing naturally, have, within the cells of the root cortex, fungal hyphae with a very characteristic appearance. Noël Bernard found that seedlings of *Neottia* had similar endophytic fungi and surmised that the well known difficulty of germinating orchid seeds was due to the necessity for fungal infection. This he tested for a large number of genera and found that with the appropriate fungus germination was more or less a matter of certainty. Several amateur and professional horticulturists in France, England, and Germany have adapted Bernard's results to orchid growing on a large scale. The fungi are isolated, grown in pure culture and the seeds sown on them. The results are striking. Bernard interested himself in the method by which the fungus acted and concluded that it was by raising the concentration of the cell sap. He used salep agar as his medium, and by increasing the percentage of the salep was able to germinate seeds of *Cattleya* without the intervention of a fungus. Since his day Baillon, Blutel, Clement, Knudson, and others have published accounts of their success in raising seedlings in the absence of fungi. In Europe the efficacy of any method is best judged by its results with *Odontoglossum*. It has been abundantly shown that this genus is susceptible to this treatment and it would probably be safe to say, generally, that orchid seeds can be germinated without fungal aid, given certain conditions.[2] It has been questioned whether seedlings so germinated would thrive and produce healthy plants and satisfactory flowers. Plants raised in this way, however, appear to be "normal" and there is no apparent reason why they should not flower. The matter, however, is one which will be satisfactorily settled only by experience

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, August 19, 1926.

[2] Knudson (Bot. Baz. **77**: (1924) p. 212) writes: "Ramsbottom .... states that while the [nonsymbiotic] method may be useful in the germination of *Cattleya* and related forms, it will not prove successful for the seeds of *Odontoglossum* and related genera." He is mistaken. Neither in the paper to which reference is made, nor in any other, have I stated this or even suggested it.

FIG. 1. *Neottia Nidus-avis.* Transverse section of root showing mycelium mostly in a clumped condition. ×30. Beech wood, Sussex.

[All figures are of longitudinal sections unless otherwise stated.]

FIG. 2. *Phalaenopsis Rimestadiana.* Transverse section of root (1 inch from tip) from pot. Shows fungus in sectors, presumably owing to separate infection from the soil. ×6.

FIG. 3. *Disa grandiflora.* Root. ×45.

FIG. 4. *Vanda suavis×Sanderiana.* Seed. ×180.

—not by discussion. So far the facts seem clear and I would suggest that the modern results follow as a normal development of one set of Bernard's ideas.

The problems of the mycorrhizal habit are among the most fascinating in the field of botany and the attention which is now being given to the peculiar relations between green plants and fungi will add much to our knowledge of many branches of biology. The interaction between two organisms must be studied in every instance as a separate problem. It differs in different forms and there is also a time and space relation in one and the same example of

FIGS. 5, 6. *Vanda suavis×coerulea.* 5. Infected seedling 14 days after sowing. Stained with eosin and showing a difference between young and old hyphae. ×180. 6. 48 days after sowing. Growing point of stem, and young leaves on left.

FIGS. 7, 8. *Calanthe.* 7. Seed. [Inverted.] ×180. 8. Seedling 8 days after sowing. ×30.

symbiosis. The altruistic implication so frequently postulated for these unions serves to fog ideas and, for the time at any rate, should be ruthlessly eliminated from all discussions. If we use the term symbiosis it should mean merely that two organisms of different affinities live constantly in close association. Presumably the fact that they do so live presupposes some reason for it; but that it is invariably for mutual benefit is an idea that would appeal to few mycologists, and fungi are the most frequent symbionts.

Professor L. Knudson, who has been prominent in the investigations of the "non-symbiotic" germination, puts a totally different interpretation on
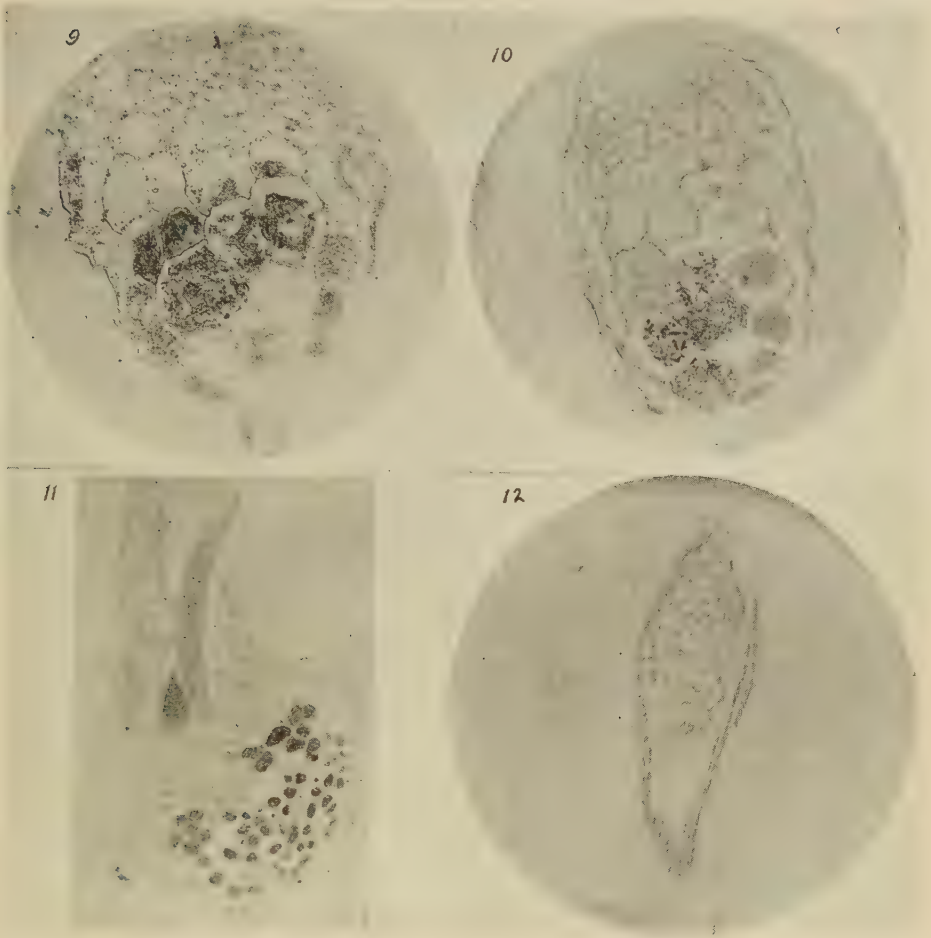
Fig. 9. *Stanhopea oculata*. Seedling 12 days after sowing. ×180.

Figs. 10, 11. *Bletia Shepherdii*. 10. Seedling 8 days after sowing. ×15. 11. Seedling 6 weeks after sowing. ×15.

Fig. 12. *Epidendrum vitellinum*. Seed ×180.

the facts from that adopted by Bernard, Burgeff, and other workers, and one which in my view is not supported by them.

Nothing is easier than to give a wrong impression by quoting an author's own words. The following extracts from Professor Knudson's papers are given, however, with the idea of plainly stating his point of view. In 1922 (Bot. Gaz. 73: [p. 2]) he writes, "Granting for the present that a symbiotic relationship exists between the fungus and the embryo, it is nevertheless true that failure of germination is more common than success, even when the fungus is provided. Bernard's experiments reveal case after case in which the introduction of the fungus was followed by death of the seeds or failure to germinate. He
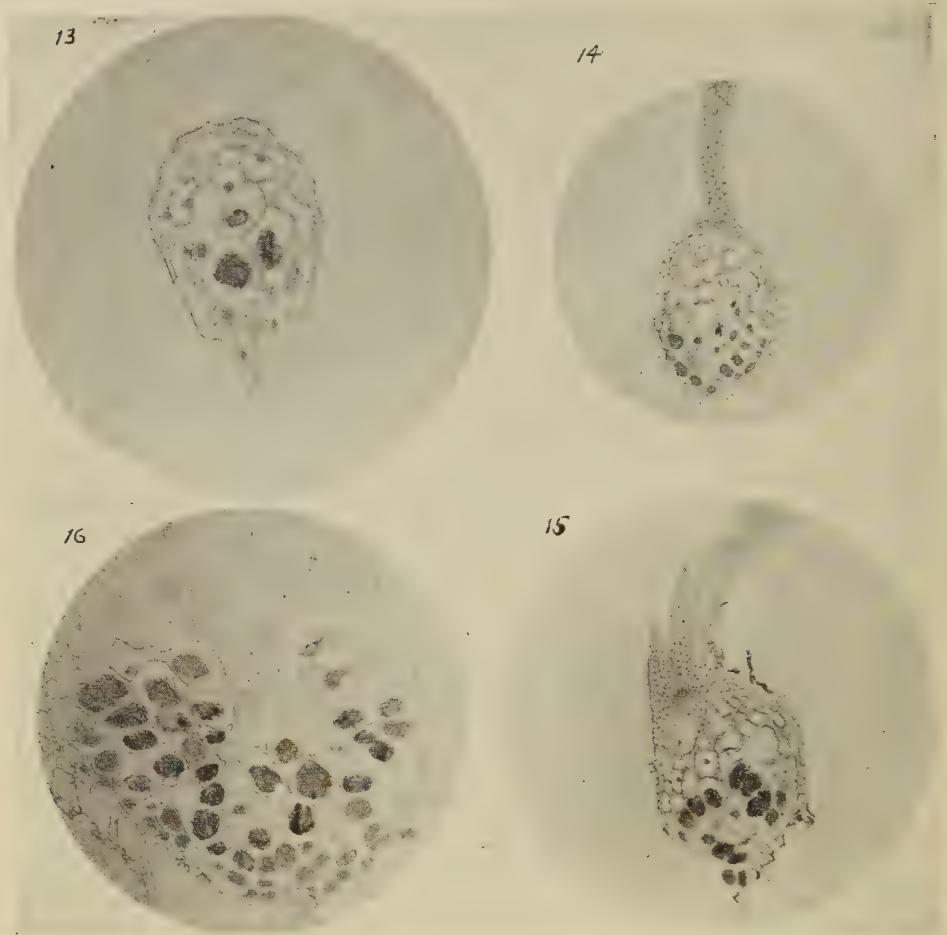
FIG. 13. *Epidendrum vitellinum.* Seedling. ×180.

FIGS. 14–16. *Disa grandiflora.* 14. Seedling 24 days after sowing; 15, 27 days after sowing; 16, 2 months after sowing—shows beginning of root formation, the young root passes through the fungal zone. All ×45.

states as follows: 'The germination by inoculation is not obtained without certain difficulties. For five years I have sown seeds of diverse species of orchids in culture tubes, each of which contained 100 seeds, and these I have inoculated with *Rhizoctonia* obtained from the roots. Altogether, I have obtained a few hundreds of seedlings, but I underestimate when I place the number of seeds used in my experiments as 50,000. For the majority of the seeds, the association with the fungus that I have placed in their presence has been merely passive and without effect, or impossible, or rapidly injurious to the embryos.' " Discussing his own results (p. 19) Knudson says, "What is the significance of these results in relation to the views advanced by

Bernard and Burgeff, and quite generally believed today, that for the germination of orchid seeds infection of the embryo by the appropriate fungus is essential?" "It is possible that the fungus, instead of being an aid in normal germination, is a factor in the death of the embryos and consequently in the failure of germination. . . . . The evidence is conclusive that under conditions of pure culture employed by both Bernard and Burgeff germination of the seeds is dependent on the fungus" (p. 23).

In a more recent paper (Bot. Gaz. **79**: 1925) Knudson considers certain of the criticisms which have been brought forward in opposition to his theoretical conclusions. Again he makes statements which call for comment. "The evidence presented by these and various other experiments leads to but one conclusion, which is that the fungus is not necessary for germination, at least for seeds of *Cattleya*" (p. 348). "The experimental basis for the symbiotic view is based entirely on the use of such media [containing either starch or sugar] in the culture work" (p. 362). "The association of fungus and root may be merely incidental and not of any significance" (p. 373). "*Phytophthora* sp. [isolated from Easter Lily] is about as favorable to germination as the orchid fungus. . . . . Germination was effected by other fungi" (p. 372). Knudson's idea is that the fungus brings about changes in the medium with the production of sugars and that it is these which are efficient in inducing any germination that may occur.[3] It seems to me that the general problem is thus entirely misunderstood. It is not a matter of how certain ends can be attained in the laboratory but what may reasonably be supposed to occur in natural conditions. As everyone now knows, excellent results are obtainable by replacing the action of the fungus. I had the pleasure of showing cultures, as fine as any I have seen, before the British Mycological Society and the Linnean Society of London in 1924, on behalf of my friend, Mr. E. Clement.

There appears to be no doubt that, according to Knudson, the explanation of the failure of orchid seeds to germinate when provided with all the conditions that permit of the germination of most seeds, is to be found in the organic food relations. Have we any grounds for believing that normally germination occurs by the action of a particular fungus on the seed itself or do we happen to have certain fungi in orchid houses which are well adapted to the Bernard method of culture? Is it that seeds have germinated and plants thrived in soil prepared for them by certain fungi and that these happen to have been distributed with the plants throughout Europe and that a pseudo-natural association between cultivated orchids and fungus has arisen—or is the association something more than that? Do orchids growing in natural conditions differ radically from those growing in orchid houses?

It is common knowledge that orchids growing wild have fungal mycelium in their roots. The exceptions which have been recorded are so very rare that either the conditions under which the plants grew were peculiar or there was malobservation. Cultivated orchids also generally show a similar infection (Figs. 1, 2). The fungus always has a particular distribution in any given

[3] "It would seem that other substances are more effective" (p. 379).

species of orchid; only certain layers of cortical cells are occupied. The fungus is not distributed in a way which is usual in diseased plants.

The fungus has a peculiar manner of growth. The mycelium more or less completely fills a cell before passing on to the next. There are several interesting facts about odd genera like *Gastrodia* which may be left out of the present discussion. When we turn to consider orchid seedlings we find a somewhat similar state of affairs. Seedlings occurring naturally are not frequently encountered. In most of the early accounts of orchid seedlings (for example, Link, "Icones selectae," 1840) peculiar inclusions are mentioned which, as Bernard pointed out, are without doubt fungal hyphae. Bernard first described endophytic fungi for seedlings in *Neottia* and later for others, and many investigators have confirmed the fact that seedlings occurring naturally have fungi in their cells. So far as my experience goes I have never found seedlings of British orchids—*Orchis Morio, O. mascula, O. maculata, Habenaria viridis, Ophrys apifera*—which did not have fungal hyphae of what may be called the usual type in their cells. Stojanow (Flora N.F. **9** (CIX): (1916) pp. 1–28) records them in *Orchis Morio* and other European species and during this year Mercier (Rev. Sci. 64th year (1926) no. 8, pp. 244–247) has reported that in Brazil he found very young seedlings, though very rarely (only fifteen in four months, though he made special search for them) of *Bifrenaria, Epidendrum, Laelia, Maxillaria* and *Oncidium*. Concerning these he states, "Les ayant examinées au microscope, j'ai trouvé dans toutes, sans exception, des champignons endophytes, sous forme de pelotons plus ou moins vivants."[4] Though there is not the amount of evidence for seedling infection that there is for root infection it suggests itself that it is just as usual and is moreover normal in that these seedlings develop into healthy flowering plants which produce seeds. Similarly in seedlings raised in the old way on pots I have always found infection except in a few cultures of *Disa* and *Sobralia*. (It could not be surmised with certainty what the future of the seeds which were sectioned would have been.) Grown on what is called the "pure culture" methods, seedlings again show the fungus within the cells of the seed. Moreover, the fungus grows in a characteristic way and is restricted in its distribution, no matter whether seedlings are taken from their natural habitat, from pots in orchid houses, or grown in flasks, and the infection in the three classes appears to be of the same type. So far as one can tell the fungus in the seedling is similar in every way to the fungus in the root of the parent plant, and it is impossible to distinguish between them. Further, the same fungus always appears to be associated with the same orchid. It is surely more than chance distribution of Cattleyas by professional growers that leads to Bernard, Blutel, Potin, and others in France, Burgeff in Germany, Charlesworth and myself in England, and Knudson in the United States, all obtaining the same (morphological) fungus from this genus of orchid. The same fungus is always present in *Cattleya* roots and is distinguishable in culture, even with the naked eye, from a culture of the fungus from *Odontoglossum*.

[4] It is possible to argue that seedlings were rare because of the pathogenic action of the fungus but infection was always found and was of the usual type.
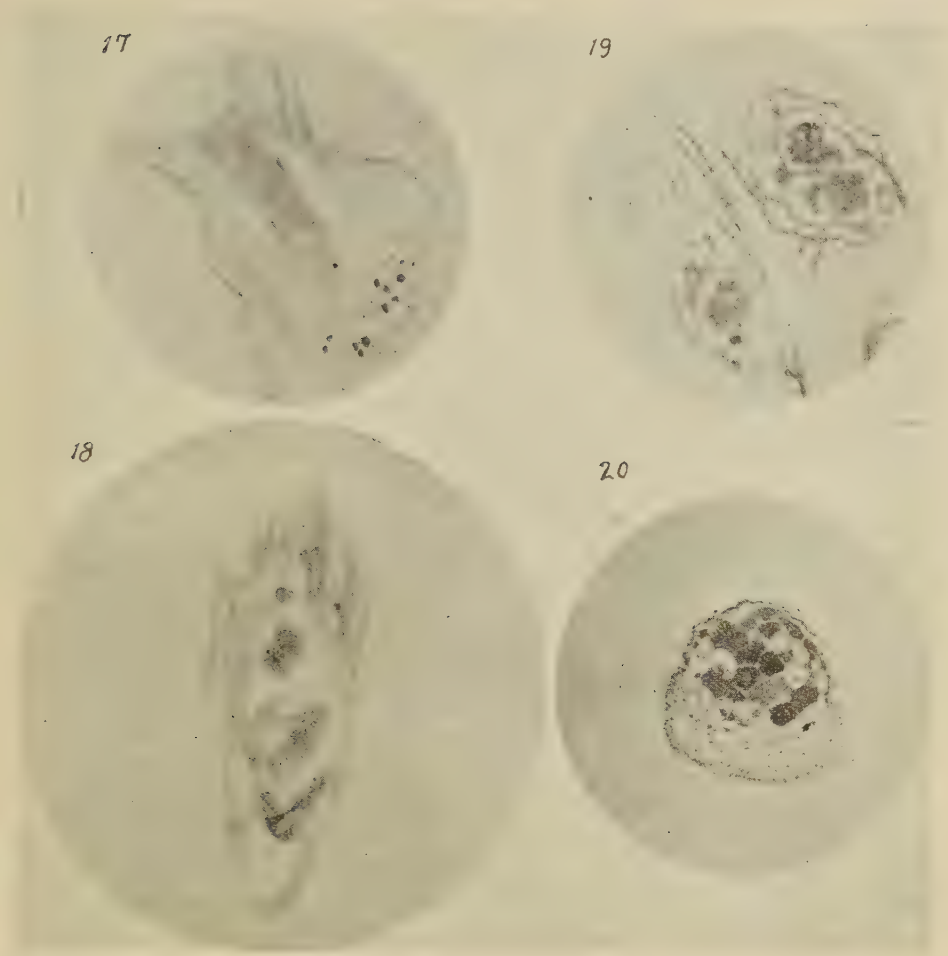
FIG. 17. *Cattleya*. Seedling 2 months after sowing. T.S. root. ×30.

FIGS. 18, 19. *Odontoglossum crispum*. 18. Seedling sown 11 days. Showing passage of hyphae into seed. 19. 14 days after sowing. Both ×180.

FIG. 20. *Miltonia Bleuana×Odontoglossum Dora*. 27 days after sowing. [Inverted.] ×45.

The fungus extracted from an orchid and grown in culture will bring about the germination of its seeds in conditions where, without the fungus, germination does not occur. Speaking generally, there are several main types of orchid fungus. One type is necessary for one or more nearly related genera; a second type is ineffective from the standpoint of germination.

Seeds germinated *in this way*, with abundant infection of the cells of the "protocorm" (and of the root) flower normally and are in every way satisfactory as horticultural plants. With the appropriate fungus germination of seed is more rapid and produces bigger seedlings than occurs on any medium of which the composition has so far been divulged. (I do not suggest that this will always hold.)

The very constancy of the association of the same fungus and orchid under natural conditions is sufficient to satisfy most of us that it is not merely incidental and of no significance. I have never examined *Cattleya* seedlings growing on pots without finding a fungus in them (Fig. 17). In England, however, *Cattleya* is regarded as exceedingly easy to grow; no one ever seems to have difficulty with it. This may be due either to the fungus being very widespread in orchid houses, or to the food necessary for germination being more easily obtained than it is in other genera, that is, that the seed is less dependent on the fungus for germination. However this may be, it is interesting that Charlesworth and I had the same experience with our first isolation of the *Cattleya* fungus twelve or thirteen years ago as did Bernard. Since at that time as many seedlings as were required were obtained from pot cultures, no further attention was paid to the matter for some years. Then when it was advisable to standardize the methods of culture several isolations of the *Cattleya* fungus were made. These fungi varied to a great extent, and with the first two or three sets of them no great success in germination was attained. It was, however, by that time well known to us that definite strains of these fungi occur, similar to those found in many other species. After a short time a strain was isolated which gave a totally different picture for *Cattleya*. Here germination occurred in a most astonishing way whether the seeds were sown on inoculated agar or on potting compost. Given seeds which are not too old, whether of bigeneric hybrids or natural species of *Cattleya* one could almost guarantee to obtain over 90 per cent germination with one of the *Cattleya* fungi in Messrs. Charlesworth's Collection.[5]

The occurrence of different strains of these orchid fungi raises many problems. Cultures sometimes are different even to the naked eye, and from a grower's standpoint are labelled "good" and "bad." I have at present no information about them except that they occur. Much can be made of their existence. They might be considered to show that the relation between orchid and fungus is very casual or very close. The phenomenon of "sectoring" also occurs in some strains of the fungus but is only apparent in Petri dish cultures and is consequently easy to overlook.

The fact that an orchid fungus sometimes kills seedlings has been very much overemphasized. It is not a very difficult matter to arrange an experiment to bring this about but in the usual method of germinating seedlings by means of the fungus the killing of seeds is an extremely rare occurrence. I have examined thousands of culture flasks and do not remember to have seen any with noticeable destruction during the last seven years or indeed at any time except under conditions of experiment. In some flasks, germination is for some reason or other not satisfactory. To assume that here the seed is killed by the fungus is an assumption and nothing more; often the fungus enters the seed in very

[5] It is necessary to make the proviso that the seeds must contain embryos. Hybrids of cultivated orchids often behave peculiarly, and one may find a seed capsule that contains mostly chaff, that is, integuments without embryos, just as one may have a well grown capsule which might be expected to contain hundred of thousands of seed having so few that only intense searching reveals them.
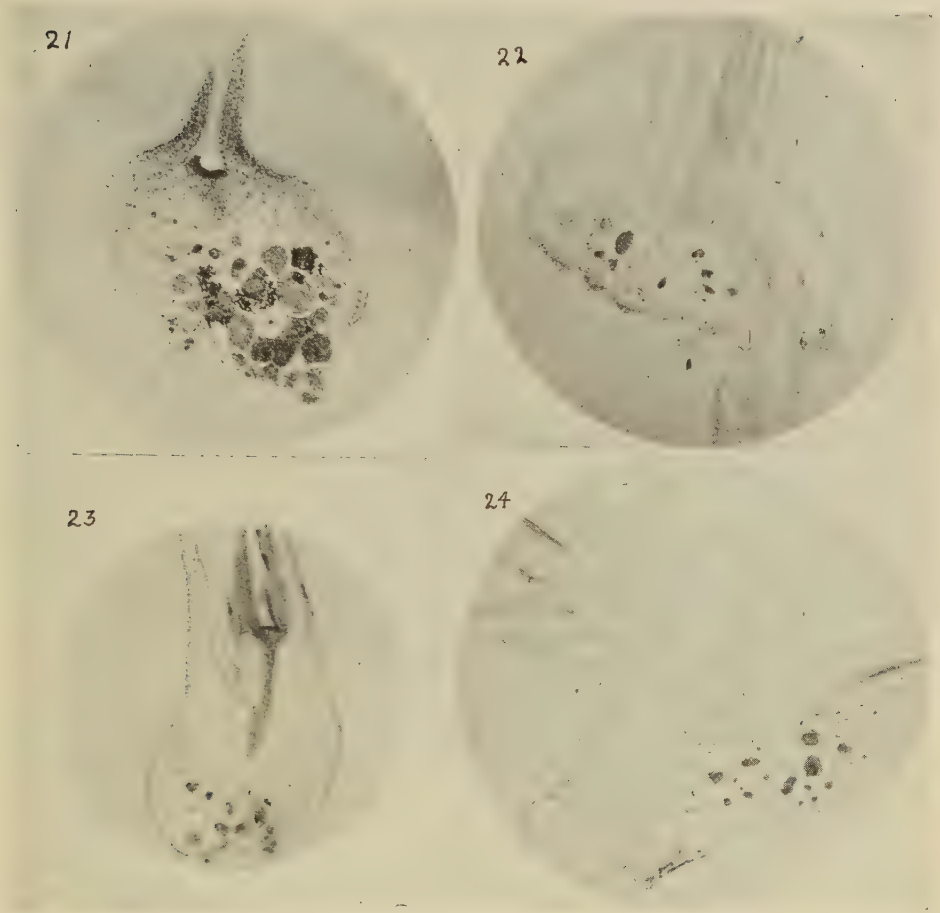
FIGS. 21–24. *Odontoglosum crispum.* 21, seedling 62 days after sowing, ×45; 22, same 92 days after sowing, showing young stele, ×30; 23, L.S. of root passing out of "protocorm" in an uninfected condition, ×15; 24, T.S. of similar root, ×15.

small amount and does not develop in what one has come to consider the normal manner.

Knudson's statement that a species of *Phytophthora* is about as effective as the orchid fungus in inducing germination is startling until it is realised that "in no case was there any embryo or seedling infected." "The strikingly beneficial effect of *Phytophthora* and the orchid fungus, therefore, could not have been due to any internal action of the fungus." I have no doubt that the explanation of the way in which the medium is altered with the production of substances capable of bringing about germination is the correct one. It is not unusual to find contaminations in culture flasks and sometimes these cause damage to the seedlings. Most of the workers on this problem occasionally have found, particularly on agar media, contaminations which appear to have a

beneficial effect on growth. Servattez when growing the moss *Phascum cuspidatum* in culture observed that a species of *Oospora* activated growth.

Under certain conditions of experiment Knudson found that his fungus did not enter the seed; in fact, he infers that it is better for the seed if the fungus is kept out of it. It is not easy to collate statements made in different parts of the same paper, but my general impression is that his belief is that external change of medium is all-sufficient and infection by an endophytic fungus either mere chance or a definite disease, the constancy of the parasite being analogous to specialized parasitism.

Without attempting to define "normal," "natural" and "necessary" I would invite attention to the photographs accompanying this paper. Only the sections of *Odontoglossum* (Figs. 18–24) were cut from seedlings in culture flasks, the others (Figs. 2–17) were all taken from the surface of compost in pots. In other words, though all show a general resemblance only certain of them have been subjected to the Bernard method of culture.

No comment is necessary on the structure of orchid seeds beyond the statement that the embryo is usually undifferentiated or nearly so. In the seeds I have examined in section there is frequently a difference in the size of the cells, those at the suspensor end being the larger (Figs. 4, 7, 12, 15). The fungus always enters the seed by the suspensor end (Fig. 18). It is almost unnecessary to state that the seeds are not sown in any definite way but take up every possible position. Nevertheless, the mycelium invariably makes its entry at the same spot. There is no precise information about the presence or absence of toxic substances in the cells at the opposite end of the seed but the non-infection of these cells both at this period and later is one of the most striking features of germination. The fungus when it enters the seed always behaves in the same way in the genera here described. It does not pass through the cells of the seed as is the most usual or possibly the invariable mode of growth of a parasitic fungus, but grows in a tangled manner, filling one cell before passing on to the next, and remains restricted to the cells at the suspensor end (Fig. 5). In considering the suggested pathogenic nature of the fungus, it should be stated that this cannot apply to seedlings transferred from pots to flasks.

It is possible to examine seedlings of which the history is known at different stages and consequently there is little doubt about the result of the infection. The sections of seedlings figured, from flasks, are in every instance from cultures concerning which there was no dissatisfaction from a grower's point of view. There is no support whatever for the statement that intensity of infection leads to the killing of the seedlings. Further, seeds which adhere to the sides and the top of the flasks germinate if fungal hyphae grow up over the surface of the glass and reach them. Knudson, commenting on Burgeff's statement that this occurred in some of his cultures, suggested that possibly the embryos were in contact with droplets of the agar medium adhering to the surface, or that the seedlings had become detached accidentally from the slope and flipped to the side of the tube. Later, reporting on some experiments, he states that embryos adhering to the side of the tube out of contact with the agar became infected but do not

germinate. I have not yet devised a method by which germination has been induced by the fungus which is not open to the objection that some of the soluble products of the medium might have reached the seeds by capillarity, though the chances of this are remote. The fungus undergoes obvious changes after it has entered the seed and finally "clumps." To me the phenomena, described by several writers, attending the process are sufficiently peculiar to suggest some particular relation between orchid and fungus. The clumping is well shown in figures 11, 13, 16, and is first seen in the cells which were first infected. That the younger portion of the fungus is still in an active condition can be seen in several of the photographs (for example Fig. 5). The differences in the mycelium are well brought out by staining with eosin. It is the balling of hyphae in the cells at the suspensor end, their ultimate clumping, and the evasion of the cells which are to undergo rapid division for the production of the stem growing point and the stele, that characterizes normal infection. A further point shown in the photographs is the way in which the young root remains free from infection (Figs. 23 and 24). In some genera (*Vanda, Odontoglossum*) the rootlet grows out away from the infected area, whereas in others (*Disa, Calanthe*) it grows right through the region. At this stage the endophyte is usually clumped and consequently not in an active condition. The fact remains however that I have never seen a young rootlet infected until it has entered the soil. All the genera which I have examined appear to have a well developed exterior wall to the root but that this is not a barrier to the passage of the fungus is apparent from the fact that the infection takes place sooner or later through this layer.

The difference between Professor Knudson's present point of view and that of other workers is perhaps not so great as it was. An orchid seed is a small specialized type of seed which is unable to germinate under conditions that suffice for ordinary seeds well provided with reserve food material. The symbiotic view is that a special fungus which enters the seed supplies the necessary "stimulus" to germination. Knudson's view is that many fungi (including the special fungus) have a "stimulating action" by producing from the substratum some form of sugar which enables the seed to germinate. In my own experiments on non-symbiotic germination I have found it necessary to follow the practice of other investigators and sterilize the seeds before planting them, for otherwise such a crop of moulds is obtained that germination is generally out of the question.[6] In considering what is probable under natural conditions it seems necessary to take this into account for it is self evident that we cannot postulate sterilized seeds falling on either sterilized media containing sugars in the appropriate amount or on one which has been satisfactorily prepared by the haphazard occurrence of fungi capable of bringing about changes in the substratum similar to those found to be necessary for successful germination in the laboratory.

The photomicrographs were made by Mr. E. H. Ellis of the Botanical Department of the British Museum from preparations made by the late Mr. Joseph Charlesworth which are now in the Department.

[6] In the symbiotic method the seeds are sown without sterilizing them.

RESEARCH METHODS IN THE TAXONOMY
OF THE HYMENOMYCETES[1]

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When macroscopic features fail to identify with satisfaction a given fungus, the careful student, anxious to attach to his plant a valid name, always has recourse to the microscope. The day is long since past when superficial observation can yield adequate identifications for any considerable number of fungi. More and more we are coming to rely on the minute detail of characters that the microscope reveals. Perhaps students of the Myxomycetes first led the way in this respect, closely seconded by the uredinologists, and in more recent years by workers in other fungous groups. Even the flowering plants are beginning to receive their share of attention of this sort, as witnessed by the recent work on plant pollen in which it has been shown that plant families can easily be recognized on the basis of the morphology of their pollen. Even generic identifications are promised for the near future. To some extent our terminology is becoming confused and distorted, often by workers without adequate conception of how properly to manipulate their terms. In order to stem this tide of irrational taxonomic terminology, and as conducive to clear thinking on the subject, it is necessary that we frequently pause long enough to set down and summarize the status of our subject matter. Such then is the "raison d'etre" for the present discussion dealing with certain microscopic features of that great group of the higher fungi known as the Hymenomycetes.

For my purpose it is not necessary to define the limitations of the group further than to recall that it includes, or may for our purpose be considered as including, those fungi that our systems of classification place between the Rusts and Smuts on the one side and the puffball group and its allies on the other. Here, in its essentials, is a group that is remarkably homogeneous, yet presenting a fine array of the more detailed microscopic characters, the use of which opens up a new world to the mycological taxonomist. It has long been recognized that in this group lie some of the most difficult of all fungi to identify satisfactorily. This is especially true of the resupinate members in such genera as *Corticium, Peniophora,* and *Hymenochaete* of the Thelephoraceae; *Hydnum, Grandinia, Odontia, Radulum,* and others of the Hydnaceae; and in *Poria, Solenia, Merulius,* and other genera of the Polyporaceae. In the absence of those

portions of the fruiting bodies usually known as stem (or stipe) and pileus (or cap), there is left in these genera only a small, thin, effused crust representing the sporophore. For years the genera mentioned, and others of similar nature, were ignored by mycologists for no other reason than the paucity of easily observed characters on which to build a classification that would separate out in an adequate manner those species, which although often of great similarity in external appearance, yet in their internal structure are as different as are species in any other group of plants. Yet for many years a few venturesome individuals, inspired by a vision of ultimate usefulness, had labored incessantly to bring order out of chaos in these groups. Truly it was a labor of love for them, some of whom have spent the leisure hours of a lifetime in a painstaking endeavor to lay the broad foundations on which others might build an adequate conception of the relationships that exist in these groups of plants. In this field the most productive American work has been done by that eminent mycologist, Dr. E. A. Burt, who is just now finishing a life's work on the members of the Thelephoraceae. And I think I do not minimize in the least the magnitude of the work of others in different groups when I say that the mycological world has rarely seen, and may not again see for many years to come, the equal of this monumental work, for painstaking thoroughness and attention to details, in a group where superficiality yields absolutely no returns on the investment. Only a few individuals are gifted with the native possibilities sufficient to carry to a successful conclusion a work of this sort.

The methods by which work of this type is accomplished are not intricate—in fact they are extremely simple. They have already been outlined in the American literature to some extent. My own methods are essentially those of Dr. Burt from whom I learned them. They can be varied to suit different situations. I outline them here only briefly, and for the sake of completeness.

Thin sections must be cut free hand, or by the aid of a freezing microtome. The last named instrument I do not use. All of the photographic illustrations that are used in this discussion are made from free-hand sections, and the drawings were outlined under the camera lucida from sections of the same kind. The rotary microtome is almost useless in work of this type. The simple process of wetting the material, first in 95 per cent alcohol (to drive out the air), and then in water until softened, yields sections that cannot be matched by those from the microtome. As the sections are cut they are transferred to a drop of KOH (5 to 10 per cent) on a glass slide. In those fungi with brown context, as for example, brown Polypori, Hymenochaetes, etc., in which KOH turns the sections dark, lactic acid may be substituted but cannot be followed by the eosin stain. The KOH, if used, should be drained off and a drop of dilute eosin stain added. Dr. Burt uses an alcohol-soluble eosin. I find the water-soluble type more advantageous since the tissues are not dehydrated by the alcohol and retain the swollen condition imparted to them by the KOH. A cover slip is added and the sections are ready for observation. All measurements should be made on material at this stage, since later, if the slides are preserved, shrinkage occurs. Sections cut and mounted in this way show fungous tissue in a remark-

able state of turgidity, comparable to that of fresh material. I have repeatedly demonstrated spores on basidia in material kept in the herbarium for 40 to 100 years.

After the stain has been allowed to act for several minutes the sections may be made into permanent mounts. A drop of slightly acidulated glycerine (two-thirds strength, diluted with water) is run under the cover glass, the excess stain and water being drawn from the opposite side of the cover slip by means of filter paper. Immediately one or more drops of 10 per cent acetic acid should be drawn under also and either allowed to remain for several minutes, or the edge of the cover slip should be raised slightly to insure the sections being thoroughly acidified. This acidification process is the crucial point in the procedure. Sections insufficiently acidified will quickly lose their stain when filed away. After the acid has set the stain, more glycerine is run under, and the slide, properly labeled, set aside to allow the water of the glycerine to slowly evaporate. This process may be prolonged for weeks or months, my own method being usually to allow slides of this type to accumulate for about six months. When it is desired to complete the mount, more glycerine must be added to replace the water lost by evaporation. The slides are then cleaned and sealed with gold size by the aid of a turn table. It is advisable to make a second seal after an interval of a week or longer. Other mounting media may be used in place of the glycerine, and other ringing materials than gold size. But I have found these so uniformly satisfactory that I have never felt inclined to experiment to any extent. A certain very small percentage of slides so treated develop defects after a few years, but it is doubtful if this could be eliminated by any method of procedure.

It is not my purpose to discuss all of the microscopic features made visible by the use of this method. Some of them are too well known and too fundamental in our classification to need repetition here. For that reason a discussion of basidial characters, for example septation and spore characters, is omitted, but must not be thought of as unimportant on that account. The material presented is to be regarded as a summary of the status of internal structure in its relation to identification rather than as adding anything to our knowledge of that subject. I shall confine my remarks to the following types of characters:

Conspicuous Sterile Bodies	Hyphal Characters
Cystidia	Diameter
Setae	Clamp Connections
Gloeocystidia	Branching
Vesicular Cells	Septation
Paraphyses	Incrustation
Conducting Cells	Tissue Differentiation
Hyphal Pegs	Zonation
	Gelatinization
	Crystalline material

These subjects do not exhaust the category of microscopic structures but they do, it seems, include the majority of them, and those that have been found to be most important.

I. STERILE ORGANS

1. CYSTIDIA

The term cystidium is too well known to require definition, yet they are not always easy to distinguish from other types of sterile organs. At the same time the term is so broad that it is really difficult to define. It includes a considerable variety of conspicuous sterile bodies not falling readily by definition into the groups to be later discussed, such as setae and vesicular bodies, yet conspicuous enough in character to differ from what are generally termed paraphyses. As a matter of fact it is difficult to draw a satisfactory line of demarcation between these two latter types of structures. Perhaps more can be deduced from the illustrations here presented than from a descriptive statement. Narrow filiform organs more or less conspicuous by reason of branching, coloration, or other features, and confined to the hymenial layer are referable to the status of paraphyses rather than cystidia. At least such is the present trend in American mycological circles, so that all bodies conspicuous by reason of size (that is, larger than the basidia), coloration, or other feature, and not possessing the characteristics of gloeocystidia, setae, or conducting organs, are usually referred to as cystidia.

Morphologically cystidia are the terminal specialized cells of undifferentiated hyphae and are usually empty or contain no visible or conspicuous content. Usually the wall is considerably thickened and often incrusted with granular crystals. The points of diagnostic value concerning cystidia are as follows: (a) *Form and Size*. In shape they vary from short conical or clavate to much elongated and subcylindric. Occasionally they have thorn-like projections on the walls as in *Pluteus cervinus* (Fig. 1). An interesting variation is found in *Pholiota acericola* where frequently cystidia with two to four sterigma-like prongs are seen (Fig. 2) that are conducive to interesting speculations as to how or from what they have originated. In *P. vermiflua* they are large and ellipsoid or subglobose (Fig. 3). In *P. ombrophila* and *P. erebia* (Fig. 4) they are cylindric with enlarged bases.

(b) *Incrustation*. Often cystidia are incrusted with a granular incrustation of crystalline material, probably calcium oxalate in most cases. Occasionally this incrusted matter is at the tip of the cystidium only, forming a cap or knob (Fig. 5). Such is the condition in an undetermined species of *Poria* in my herbarium, and in the small cystidial cells of *Polyporus abietinus* (Fig. 6). More often the incrustation covers the major portion of the cystidium as in *Poria nitida* and in many species of *Peniophora*, and *Stereum* (Figs. 7, 8).

(c) *Color*. Cystidia are typically colorless, but distinctly brown forms are sometimes seen in certain brown species of *Stereum*, for example, *S. umbrinum* (Pl. 1, fig. 1). In these cases the color resides in the wall and not in the cell content as is said to be the case in *Mycena leaiana*.

[2] In the preparation of the text figures illustrating this paper, I have had the able assistance of Miss Edna G. Stamy, senior student in Botany at the Pennsylvania State College, to whom I am much indebted for the quality of the drawings. Nearly all of the figures were originally drawn under the camera lucida at a magnification of about 820 diameters, but reduced somewhat in reproduction.
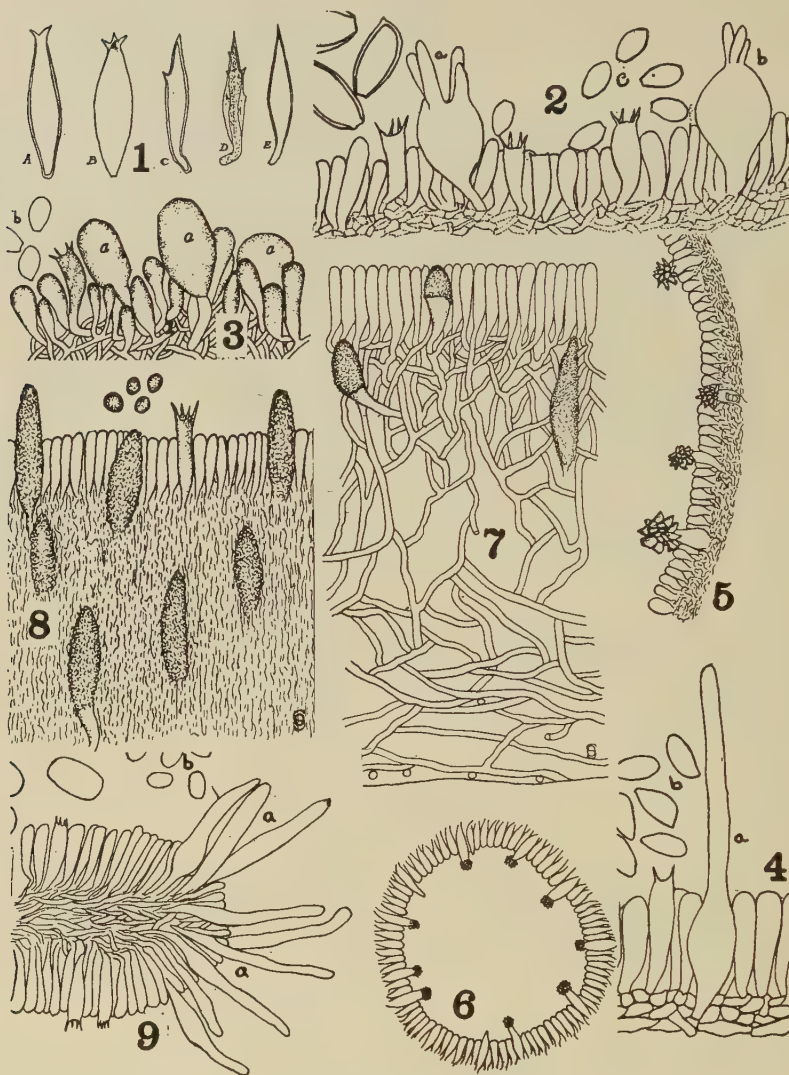
TEXT FIGURES 1–9

Fig. 1, A-E; Cystidia of *Pluteus cervinus*.

Fig. 2. Hymenial layer of *Pholiota acericola*, showing cystidia with sterigma-like projections at a and b.

Fig. 3. Hymenial layer of *Pholiota vermiflua* with large rounded cystidia, a.

Fig. 4. Hymenial layer of *Pholiota erebia* showing cylindrical cystidium with enlarged base.

Fig. 5. Hymenial layer of a species of *Poria* with cystidia bearing crystals capitately arranged.

Fig. 6. Hymenial layer of *Polyporus abietinus* with small capitate- incrusted cystidia.

Fig. 7. Vertical sections of the fruiting body of *Peniophora mutata* showing imbedded and incrusted cystidia, and a loosely interwoven subhymenial layer.

Fig. 8. Vertical section through the hymenial region of *Stereum sulcatum* showing incrusted cystidia, some imbedded, others projecting.

Fig. 9. Section of the edge of a gill of *Pholiota confragosa* showing radiating cystidia confined to that region.

(d) *Location.* Usually cystidia are at least in part hymenial organs, or if originating in the subhymenium then projecting to or beyond the level of the basidia. Occasionally they are completely imbedded in the subhymenium as in *Peniophora mutata* (Fig. 7). In *Poria subacida*, when present, they project only slightly (Pl. I, fig. 2); in *Stereum sulcatum* some are entirely imbedded and others project strongly (Fig. 8). In some of the gill fungi, they are confined to the edges of the gills where they may be inconspicuous or may project in a radiating manner as in *Pholiota confragosa* (Fig. 9).

(e) *Comparative abundance.* In *Merulius tremellosus* cystidia are much scattered, often a single section of the usual size being devoid of them or containing but a single one. In other species they may be so numerous as to make it a question where and how the basidia can be produced (Pl. I, fig. 4). All intervening conditions occur (Pl. I, fig. 3).

(f) *Septations.* Very occasionally there occur projecting cystidia-like hyphae that are relatively undifferentiated but conspicuous, and are plainly seen to be septate. Such occur in species of *Odontia* and *Grandinia*, and usually in these genera, they are localized at the tips of the granules or teeth of the hymenium (Pl. I, fig. 5).

Obviously such a variety of characteristics in a single set of organs yields an abundant opportunity for using them as points of diagnostic value. Of course, entire genera are often without them, and, on the other hand, genera are occasionally based on their presence. For example the genus *Corticium* is separable from the genus *Peniophora*, both of the Thelephoraceae, only in that cystidia are present in the former and absent in the latter. A considerable number of species of *Poria*, of *Polyporus*, of *Pholiota*, and of *Flammula*, not to mention many other genera, have cystidia in the hymenium. They, of course, become of correspondingly greater value in resupinate species where the total number of characters available is so markedly reduced by the absence of a cap or a stem, or both.

The function of these bodies has never been satisfactorily explained. Brefeld's view that they are metamorphosed basidia is borne out by the fact that they are said to contain, in young stages at least, the two nuclei characteristic of basidia; and, they occasionally, as in *Pholiota acericola*, have two to four much enlarged but quite significant sterigma-like projections. Brefeld likewise has reported cystidia of *Coprinus stercorarius* as bearing both sterigmata and spores. Wettstein reports, however, that in *Coprinus extinctorius* they contain but a single nucleus, which of course might possibly be a fusion nucleus.

The early view held by Corda, Hoffman, W. G. Smith, and Massee, that they are male reproductive organs, producing spermatozoids that fuse with the spores and so bring about fertilization, is of interest now only from a historical viewpoint, and, unfortunately for the mycologist, the view of W. G. Smith that the great variety of fleshy fungi is due to hybridization brought about by spermatozoids from the cystidia of one species fertilizing the spores of a different species cannot be used as an alibi for the often barren results in attempting to draw generic and specific lines. Even as late as 1887 Massee wrote that the

mature cystidia contain glycogen that is emitted from an opening in the apex of the cystidium and flows over the surrounding hymenial surface forming a food for the basidia. Such a function has not received credence of late years. The more recent idea advanced by Massee (1906), by Knoll (1912), by Topin (1901), and others, that at least in some species they act as water excreting cells or possibly for the excretion of certain end-products of metabolism, is more reasonable. Yet obviously all cystidia do not perform the same function. Possibly in some species they may act as a passive protection to the hymenium against the attacks of slugs and other low forms of animal life. In species of the genus *Coprinus*, particularly in *C. atramentarius*, they seem certainly to act as spacing organs for the flaccid gills, the proximal end of a given cystidium being attached to the subhymenium of one gill and the distal end firmly pressed against or imbedded in and fastened to the side of an opposite gill; there being 75 to 100 such cystidia per each square millimeter of gill surface.

Nothing has been said so far concerning the "cystidiform cells" of Knoll, present on the surface of the pileus and on the stem of *Marasmius cohaerens* and a few other species. Such unusual occurrences of conspicuous cystidial cells makes the species bearing them unusually easily identified through the medium of the microscope. Perhaps, however, they occur more frequently in such situations than our investigations have made us aware of up to the present.

2. SETAE

Setae have been defined as sterile conspicuous brown organs in the hymenium or the subhymenial tissue, differing from cystidia in their brown coloration. A further limitation of the term seems desirable to take into account a characteristic chemical component of the walls of these cells such that they become darker in KOH solution. Unless this distinction is made it becomes impossible to separate from this category certain cystidial types that can be arranged in a series of progressively lighter coloration till they blend with and are indistinguishable from very pale colored cystidia. Where this unknown chemical substance is present in the setae it is likewise present in some or all of the hyphae of the fruiting body, so that entire sections become too dark for adequate microscopic examination when immersed in KOH. To obviate this difficulty of vision it is always advisable to mount material of such a species in lactic acid which gives no comparable darkening effect. In all such cases, however, the eosin stain cannot be used since it precipitates with the lactic acid.

In form, setae are more uniform than are most of the other sterile elements of the hymenium. They are always elongate and are more or less pointed at the tips. Yet in size they vary considerably. Among the smallest known may be mentioned those of *Fomes linteus* (Fig. 10) which measure $18–21 \times 6–7\mu$, while the larger ones, such as are present in species of *Hymenochaete corrugata* measure 100 or even 150μ in length and not more than 10μ to 12μ in diameter (Fig. 11).

Points of diagnostic value concerning setae are as follows:

(*a*) *Size,* as per the preceding paragraph.

(b) *Form*, some being short, broadly conical, and very sharp pointed (Fig. 10), others more cylindric though the apex is usually narrowed to a point (Fig. 11).

(c) *Character of tip*, whether very sharp pointed or relatively blunt, and whether straight or curved. In a very few species, for example, *Fomes robinsoniae* the tips of at least some of the setae are characteristically curved (Fig. 12).

(d) *Extent of Projection*. In *Polyporus gilvus* (Fig. 13) and in *Fomes pomaceus* they are distinctly hymenial organs originating in the same region as do the basidia and sometimes not projecting beyond them. In others they project very conspicuously beyond the basidia (Figs. 11, 12). Even the general length of the projecting part may be of diagnostic value. For example *Poria ferruginosa* (Pl. 1, fig. 6) may most easily be separated from *P. viticola* (= *Trametes tenuis*) by the fact that in the former they project 15 to 30μ while in the latter they are much longer, projecting to lengths of 30 to 60μ.

(e) *Imbedded Setae*. In most species setae are hymenial organs, but in *Polyporus glomeratus*, *Fomes pachyphloeus*, and *F. lamaensis* there are large seta-like structures imbedded in the tissue of the trama or of the context, or both. In such cases they are easily demonstrated in vertical sections or in crushed or teased bits of the tramal or context tissue (Pl. 2, fig. 1, 2) or are detected in cross section by their large diameter (Pl. 2, fig. 3).

(f) *Comparative abundance*. The relative number of setae is often an important diagnostic point. While this can only be expressed in such general terms as abundant, frequent, and rare, and is a matter of degree rather than of quality, and depends in part on the thickness of the sections on which the observations are based, yet it is often a decidedly helpful point. The two extremes are readily shown in Fig. 14 and Pl. 2, fig. 4.

(g) *Place of origin*. Burt has emphasized in the genus *Hymenochaeta* the importance of the relative level at which the setae originate, some coming from the base of the basidial layer and some from underlying regions or layers all the way to the substratum.

Setae are present in a number of genera of Hymenomycetes, always associated with a brown coloration of context or trama. Ellis and Everhart based the genus *Mucronoporus* of the Polyporaceae on their presence, including such species as *Polyporus gilvus*, *P. licnoides*, *Fomes igniarius*, *F. everhartii*, etc. In fact perhaps 5 to 10 per cent of the species in the genera *Polyporus* and *Fomes* have setae. There is a considerable section of the genus *Poria* with setae. They are probably less common in the Hydnaceae and absent from the Clavariaceae and the Agaricaceae. In the Thelephoraceae the genus Hymenochaete with about 40 species is rather definitely characterized as possessing setae. A few species of *Stereum* also have seta-like organs that do not, however, darken in KOH solution and so are best regarded as brown cystidia.

The probable function of these bodies is in doubt. Undoubtedly when in the tramal tissue or the context they give rigidity to that region. That they are actually protective in function when they occur in such great abundance as in some species of *Polyporus*, *Fomes*, and *Hymenochaete* cannot well be doubted; yet even here they may have a more fundamental "raison d'etre."
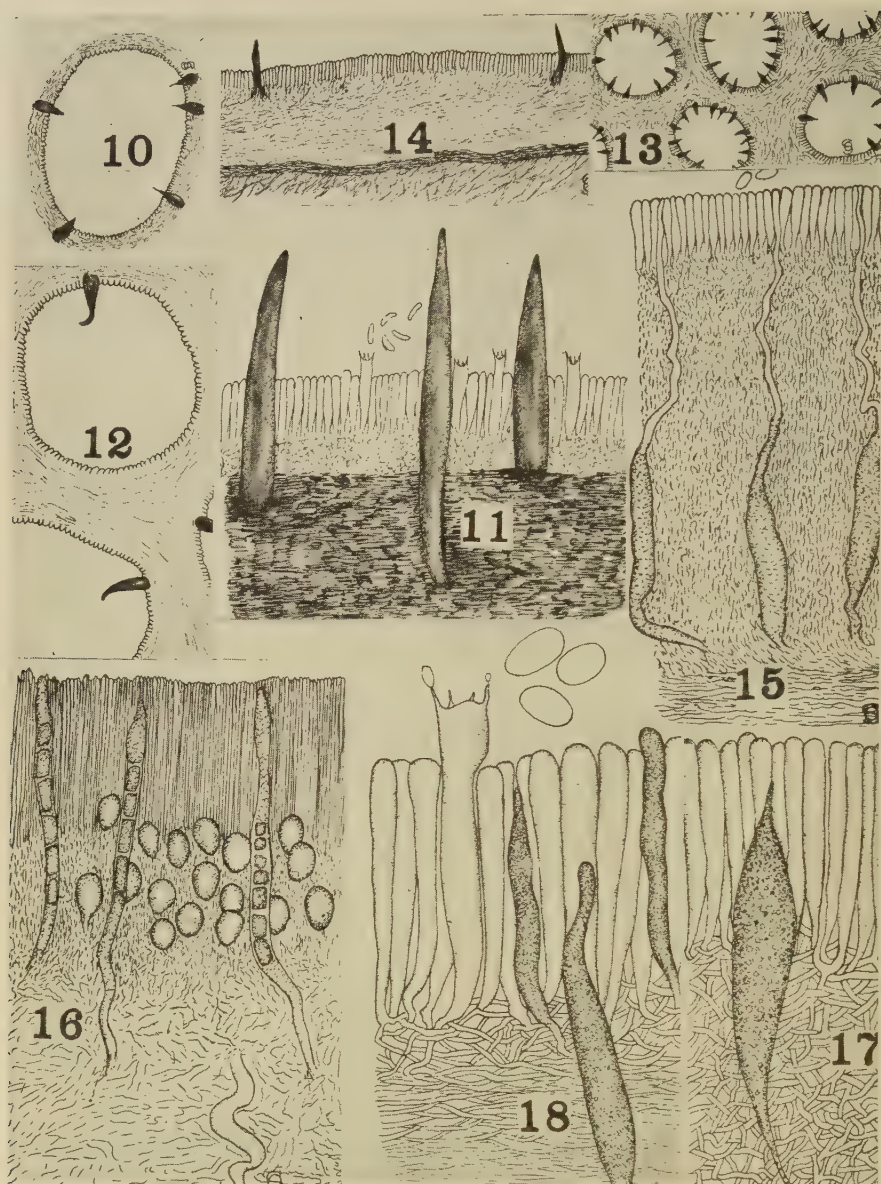
TEXT FIGURES 10–18

Fig. 10. Cross-section of a tube from the hymenium of *Fomes linteus* showing small conical setae.

Fig. 11. Vertical section of the fruiting body of *Hymenochaete corrugata* showing large elongated setae arising at different levels in the sub-hymenium.

Fig. 12. Cross-section of the hymenium of *Fomes robinsoniae* showing scattered setae with curved tips.

Fig. 13. Cross section of the hymenium of *Polyporus gilvus* showing abundant setae of small size.

Fig. 14. Vertical section of the fruiting body of *Hymenochaete curtisii* showing scattered setae and zonation of the context.

3. GLOEOCYSTIDIA

Gloeocystidia may be defined as prominent sterile organs resembling cystidia but filled with a granular or oily, often colored, material, and hence quite opaque in appearance, and from which the contents do not exude in the form of a latex when the organ is broken. In all the cases I have observed they are entirely imbedded, sometimes in the hymenial layer but more frequently in the subhymenial region (Figs. 15—18). The content in some appears densely granular, in others more liquid, resembling an oil emulsion. The walls of these bodies are always colorless as far as I have observed, all color residing in the content, which if colored is usually golden or yellowish brown. The form of these bodies is always elongated, and frequently they are curved or sinuous in outline (Figs. 15, 16). Burt has described for *Peniophora mutata* gloeocystidia of ovoid form but I have been unable to demonstrate them in that species in my herbarium, finding rather empty colorless bodies with light granular incrustation which I would refer to the category of cystidia of the usual type. Likewise in *Phlebia cinnabarina* and in *Peniophora incarnata* there are some short clavate sterile bodies that are empty and colorless and should be classed as cystidia, although gloeocystidia are also present in the latter species.

Gloeocystidia are easily seen to be the terminal cells of unspecialized hyphae. They are probably never septate, though the content may, particularly on treatment with glycerine, break up by unequal contraction into short cylindric masses that may give a septate appearance (Fig. 16). Frequently their tips are narrowed to smaller diameter (Fig. 15) and may extend from the subhymenial region to the level of the hymenium, but seldom if ever project beyond the basidia. They are easily observed in fresh free-hand sections stained with eosin, but when mounted in glycerine they, in some species, become quite transparent, seeming even to lose their content, particularly if it be of apparently liquid character, and then become relatively inconspicuous.

Two sources of error are to be watched for with regard to these bodies. In the first place, it is not impossible to confuse a type of gloeocystidium having a highly granular content with cystidia of the usual type, having fine external incrustation. With a little care, however, this difficulty is obviated in most cases and practice soon yields returns in proficiency in making this distinction. A second source of error less likely to occur is in making a distinction between these organs and the conducting organs, so called, that are present in such species as *Stereum sanguinolentum*, and *S. gausapatum*. As a matter of fact such a

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Fig. 15. Vertical section of the hymenial region of a species of *Peniophora* showing a form of gloeocystidia enlarged below and narrowed to small diameter above, the shading indicating the dense opaque content.

Fig. 16. Vertical section of the hymenial region of *Seismosarca alba* showing elongate gloeocystidia with contents separated into sections due to their being dehydrated in glycerine. The rounded bodies are basidia, whose sterigmata form the upper palisade layer.

Fig. 17. Vertical section of the hymenial region of *Stereum rufum*, showing a gloeocystidium.

Fig. 18. Vertical section of the hymenial region of *Peniophora aurantiaca* showing gloeocystidia.

distinction may not be desirable, and the more one studies these organs the closer the similarity appears. Gloeocystidia apparently do not "bleed" when wounded, while the so-called conducting cells (really a type of latex organs) do. Moreover, the walls of some types of latex organs are colored while the walls of gloeocystidia are colorless. However, it is well in both cases to base observations on unstained sections of the material in question, since they sometimes take an eosin stain with considerable avidity.

The value of these organs as diagnostic characters is seen from a consideration of the number of species in which they occur in the various genera. For example, Burt lists them as present in 8 species of *Stereum* (Fig. 17) out of a total population of about 77 species; likewise in about 22 out of 120 species of *Peniophora* (Fig. 18). In *Merulius* one species only, *M. rugulosus*, is known to possess them. Otherwise they have not been recorded for the Polyporaceae and are not known to occur in other families of the Agaricales. In the Tremellales, the fungus long known in America as *Tremella albida* and now often referred to the genus *Seismosarca*, has abundant flexuous gloeocystidia by which the plant is easily identified (Pl. II, fig. 5).

Little can be said concerning any possible function these bodies may have. I am inclined to the view that they may represent reserve bodies of stored food material. They cannot be protective in function, as are perhaps cystidia of the usual type, unless they represent accumulations of such products as would render them unpalatable to forms of animal life that might otherwise feed on the tissue of the fungus. They are not present in any species of fungus ordinarily used as food by man, so that a lack of correlation on that point is evident.

4. CONDUCTING CELLS (LACTIFEROUS CELLS)

Not much is known about the frequency of bodies of this type. I refer to such bodies as Burt has made known for a few species of *Stereum*, and these cannot be separated readily, except possibly in color, from the latex cells of *Lactarius*. They are elongate elements, not markedly conspicuous and recognizable as latex organs by their action when broken. The exuding of a white, watery, or colored juice is familiar to all in all species of *Lactarius* and may be readily demonstrated. But in those species of *Stereum* where these bodies occur, an exudation takes place only in fresh growing specimens. At other times, however, except when the plants are thoroughly dessicated, their presence is indicated by a darkening in color of the hymenium where the finger nail or a sharp instrument is drawn across that surface. Sections through the hymenium show these organs to be, for example, in *S. gausapatum* and *S. sanguinolentum* (Fig. 19 and Pl. II, fig. 6), elongate narrow bodies curving upward into the basidial layer from the subhymenium. Sometimes they extend beyond the level of the hymenium; at other times they may not reach that level. In the former species they are practically colorless, but in the latter they are decidedly brownish. They are never incrusted and their walls are relatively thin. After treatment with glycerine and acetic acid the content is distinctly opaque

and sometimes granular or broken up into opaque blocks. Since in their fresh condition the content must be liquid as evidenced by their bleeding, it is difficult to see just why they should be separated from the category of gloeocystidia, although it is evident that gloeocystidia do not exude to the surface of the hymenium in visible amounts. However, the chemical make-up of the content might be so different in the two cases that oxidation occurs when that of latex organs is exposed by wounding, while no such visible change occurs in the other case. At any rate, the appearance of these separately designated sets of organs when studied under the microscope indicates that they belong in the category of conducting cells or reservoirs for special types of liquid materials in the fungus.

In the genus *Lactarius* they are especially abundant and are found in certain species of *Mycena*. Often they are pointed at the apex and in most cases project somewhat beyond the level of the basidia. Here they are colorless, thin-walled, and free from incrustation, though in dried plants their content becomes, in some, decidedly dark, as in *Lactarius indigo* (Fig. 20).

5. PARAPHYSES

Bodies that are not readily referable to any of the preceding categories of sterile hyphal structures, yet are conspicuous enough to be noted, fall under the term paraphyses. The old conception of paraphyses as spacing organs between the basidia has been extended in recent years. In the older sense paraphyses had no special significance to the taxonomist, since all such then known were too inconspicuous to be noted. It may even be questioned whether paraphyses in that sense and as usually illustrated in elementary texts were more than immature basidia. But the more advanced conception of these organs includes types of sterile structures that cannot be so regarded.

It is difficult to draw a line at times between paraphyses of the more conspicuous type and cystidia. For example, the sterile bodies, usually capitate incrusted, in the hymenium of *Polyporus abietinus* (Fig. 6), might, at least were it not for the incrustation, be with equal propriety referred to as paraphyses. I prefer to regard incrusted organs of this type as outside the realm of paraphyses. Others of the same general type, but lacking incrustation, for example, as in some forms of *Poria subacida* (Pl. I, fig. 2) and in *P. vulgaris* (Pl. III, fig. 1) at times might be called paraphyses. Such inconspicuous organs are not infrequent along a hymenial layer that has not yet developed basidia, and their presence in abundance seems to represent a stage in the development of a number of fungi as described by various authors. Bodies of this sort are intermediate between paraphyses and cystidia.

In *Daedalea confragosa* (Fig. 21), *Stereum roseocarneum*, *Corticium galactinum*, and in some species of *Aleurodiscus* (Fig. 22a) these organs have short lateral branches that render them more or less conspicuous, yet even here, sections must often be observed with care in order to substantiate their presence. This type of paraphysis has been termed "antler paraphyses."

The most conspicuous type of paraphyses exist in some species of *Aleurodiscus* of the Thelephoraceae. In *A. amorphus* they are described as in part
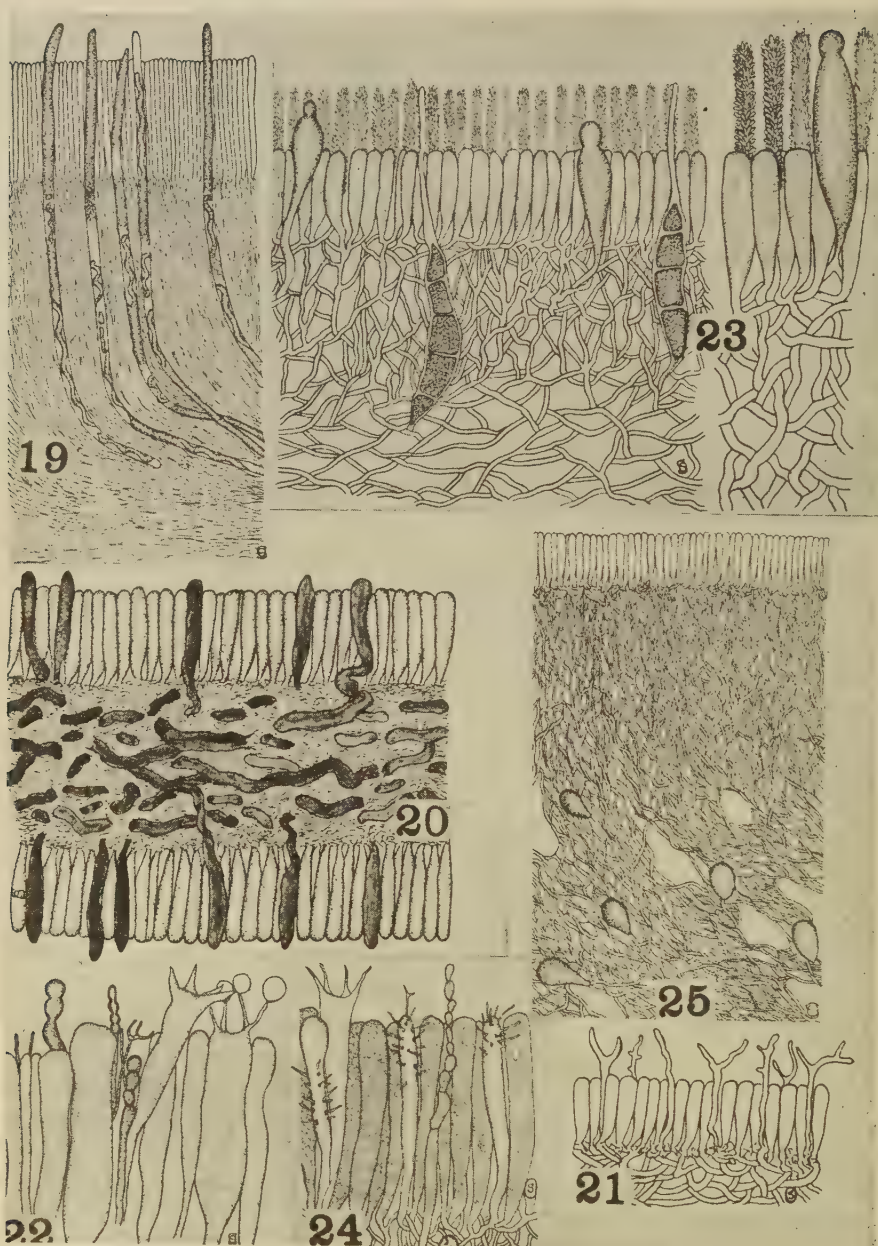
TEXT FIGURES 19–25

Fig. 19. Vertical section of the hymenial region of *Stereum gausapatum* showing elongated conducting cells with opaque content.

Fig. 20. Cross section of a gill of *Lactarius indigo* showing the dark conducting cells in the trama and extending out between the basidia.

Fig. 21. Cross section of the hymenium of *Daedalea confragosa* showing branched paraphyses of the "antler" type.

moniliform (Fig. 22b), that is, constricted at regular intervals so as to resemble a string of beads. In *A. farlowii* and *A. cerussata* they are narrow, cylindric, and thickly set with short lateral branches like a coarse test-tube brush (Fig. 23). In *A. oakesii* they are of the same general type but much larger and with coarser branches. (Fig. 24). In a few cases as in *Corticum galactinum* and *C. investiens* specimens are frequently collected in an apparently sterile condition without even the basidia formed, and in such the paraphyses form a conspicuous character easily recognized by their peculiar and unusual form.

6. VESICULAR BODIES

In the subhymenium of a few Hymenomycetes, mostly confined to the family *Thelephoraceae*, there occur pyriform or rounded thin-walled vesicles of a rather conspicuous character that are often of great diagnostic value. For example in *Stereum murrayi*, they are present in great abundance (Fig. 26 and Pl. III, fig. 2) and measure $20-26 \times 14-18\mu$. They differ from certain types of cystidial cells in their thin walls, and from other similar organs in the fact that they are always entirely imbedded. Burt records them as present in four species of *Stereum*, including the rather common *S. purpureum* (Fig. 25 and Pl. III, fig. 3). Their conspicuous character sets these species off at once as very sharply characterized.

Careful examination under the microscope gives little clue as to the significance of these bodies. They seem in some cases to be the terminal cells of undifferentiated hyphae (Fig. 25) but in other cases this cannot be made out. They are not simply cavities in the subhymenial tissue for even where completely hedged about by hyphae they often show an affinity for eosin stain, and this is so pronounced in *Stereum purpureum* that they show up quite darkly in stained sections (Pl. III, fig. 3). As illustrated in *S. murrayi* (Pl. III, fig. 2) many of them may not so appear. Definite granular bodies are found in some.

7. HYPHAL PEGS

Dr. Burt first called to my attention several years ago a type of sterile organ not uncommon in the *Polyporaceae*, yet never described by workers in that group, but seemingly of considerable taxonomic value. These are organs of cylindric or conoidal form, consisting of a cluster of closely agglutinated hyphae that project into the lumen of the tubes in that genus (Fig. 27). They are never found in the genus *Fomes*, nor in *Daedalea* or *Lenzites*. Likewise I have never seen them in true species of the genus *Poria*, nor in those species with brown context, nor in the soft white species of *Polyporus*. But in the thin *Polystictus* types of

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Fig. 22. Vertical section of the hymenium of *Aleurodiscus amorus* showing one "antler" paraphysis and three moniliform paraphyses.

Fig. 23. Vertical sections through the hymenial region of *Aleurodiscus cerussata* showing abundant projecting paraphyses with many short lateral branches; two gloeocystidia also shown; the right-hand drawing to somewhat larger scale; also shows loosely interwoven sub-hymenial region.

Fig. 24. Vertical section of the hymenium of *Aleurodiscus oakesii* showing three conspicuous paraphyses with slender branches and one moniliform paraphysis.

Fig. 25. Vertical section of the hymenium and the sub-hymenial region of *Stereum purpureum* showing five imbedded vesicular cells and their origin.

Polyporus many species possess them and they are present in a few species of *Favolus*, (for example, *F. brasilensis*) and in *Trametes serpens*. In the latter species (Pl. III, figs. 4. 5) they are large enough to be visible under a hand lens and such a condition links these bodies with those of the well known genus *Mycobonia* where they are yet larger and barely visible to the unaided eye. They never bear basidia and so must be regarded as compound hyphal emergences. Sometimes, as in *Favolus brasilensis*, they are distinctly pointed at the apex, hence of conic shape; in *P. maximus* and *Trametes serpens* (Fig. 27, and Pl. III, figs. 4, 5) they are more elongated and practically cylindric in form; and in *P. havannensis* and *P. ectypus* they are low conoidal in outline (Pl. III, fig. 6). Other species show intermediate forms. *P. versicolor* has them (Pl. III, fig. 7), and *P. occidentalis*, a tropical species, is most easily and surely separated from *P. hirsutus*, a temperate region species extending into the tropics, by their presence in considerable number.

II. Hyphal Characteristics

Not enough attention has been given the hyphae of Hymenomycetes by way of discovering differences that may be of taxonomic import. Obviously one must proceed with caution in discussing them, at least until more information is gathered concerning their variability with reference to nutrition, portion of the fruiting body from which taken, and perhaps age and growing condition as well. However, I have found, particularly in the *Polyporaceae* and undoubtedly demonstrable in the other more fleshy families as well, that hyphal characters are often of prime importance. I recall in particular an instance to the point within the last year. In a certain herbarium is deposited a somewhat undeveloped and immature collection from the American tropics, bearing the identification by one mycologist of repute as *Polyporus depauperatus*, but endorsed by another as being a different species. Since the specimen was sterile and not well developed, other microscopic characters became of prime value, and it was quickly discovered that in one of these species the hyphae of the context were distinctly septate and in the other no septa were visible with the same reagent treatment. This character immediately placed the collection in question in its proper category. I have seen instances of this sort repeated many times over. The main characters I have found of value are as follows: Diameter of hyphae; presence or absence of clamp connections; septate or aseptate; manner and extent of branching; presence or absence of incrustation. I have used these mainly in connection with my studies in the genus *Poria* and most of my illustrative material will therefore be drawn from the *Polyporaceae*.

A. Diameter of Hyphae. Hyphae vary in diameter from 1μ to about 15μ. Among the smallest are those of *Poria* (*Porothelium*) *fimbriata* (Fig. 28A), a species which when well developed simulates in appearance *P. semitincta* and others, but which is easily separated under the microscope by the small hyphae. Most hyphae have a diameter between about 2.5μ and 8μ (Fig. 28B, C) and only a few go beyond these figures, so that in the bulk of the species hyphal diameters alone are not of great service. *Polyporus obolus* and *P. tricholoma* of the American

tropics have some hyphae in the context that are 10 to 15μ or even 20μ in diameter (Fig. 28D) and by this fact they are easily separated from other similar stipitate species. But these extremes, I am convinced, do not alone represent the usefulness of hyphal diameters. I believe a careful study will show that in the intermediate ranges enough variation among species can be detected to make figures of that nature reliable when carefully used, and of course when taken in connection with other characteristics. For example, preliminary observations show that *P. lignosus* and *P. zonalis*, two species often much confused and sometimes treated as variations of the same species, can be separated in that one has hyphae never more than 6μ diameter, the other with many hyphae up to 9μ diameter. As a matter of fact, microscopic characters of less relative range are constantly used as diagnostic features of the rust fungi and perhaps as well among the Myxomycetes.

In investigating the diameter of the hyphae I invariably use small pieces of the context of the pileus or, in resupinate specimens, the subiculum. In a few cases this is virtually impossible and it is necessary to take the tissue of the pores.

B. Clamp Connections. Of recent years clamp connections have received renewed importance from the standpoint of their possible function. That they are highly characteristic of hyphae of Hymenomycetes is a well known fact. That they are universally present throughout the group has not been demonstrated and is not likely. On hyphae taken from the context or the subiculum of some species they are always and indisputably absent, even where cross walls are easily demonstrated. But in such species they may of course occur in other parts of the vegetative or reproductive phases. The presence or absence of clamp connections is an important diagnostic feature of the hyphae. For example, *Poria subacida*, *P. medullapanis*, *Polyporus versicolor* and probably all its relatives in the old *Polystictus* section of the genus, and all polypores with brown context, whether resupinate or pileate, seem to be without them.

They are most common in the sub-fleshy white section of *Polyporus* but I believe I have never demonstrated them in either *Fomes*, *Daedalea*, or *Trametes* —genera in which the plants are tough or woody and the hyphae usually thick walled. How universally they are present in the gill fungi is not known. In the *Thelephoraceae* their distribution is as variable as noted for the pore fungi.

In addition to the mere presence or absence of these curious structures, some little variation in abundance and in extent of development exists. Such species as *Polyporus caesius* (Fig. 29A), *P. biformis*, *P. fumosus*, and *Poria myceliosa* have large, conspicuous, and well developed clamps. On the older and more indurated hyphae crushing out the mounts causes many or nearly all of the hyphae to break at the clamps, so that the broken end of the hypha shows a hooked appearance where the clamp remains attached. In a few species this is often about the only condition in which they can be found. At the other extreme in point of size are those of *P. mucida* (Fig. 29B), so inconspicuous as to be easily passed over on superficial examination. *P. mucida* is so easily identified on this one characteristic alone that in case of otherwise doubtful identity the demonstration of these very small clamps is all-sufficient.
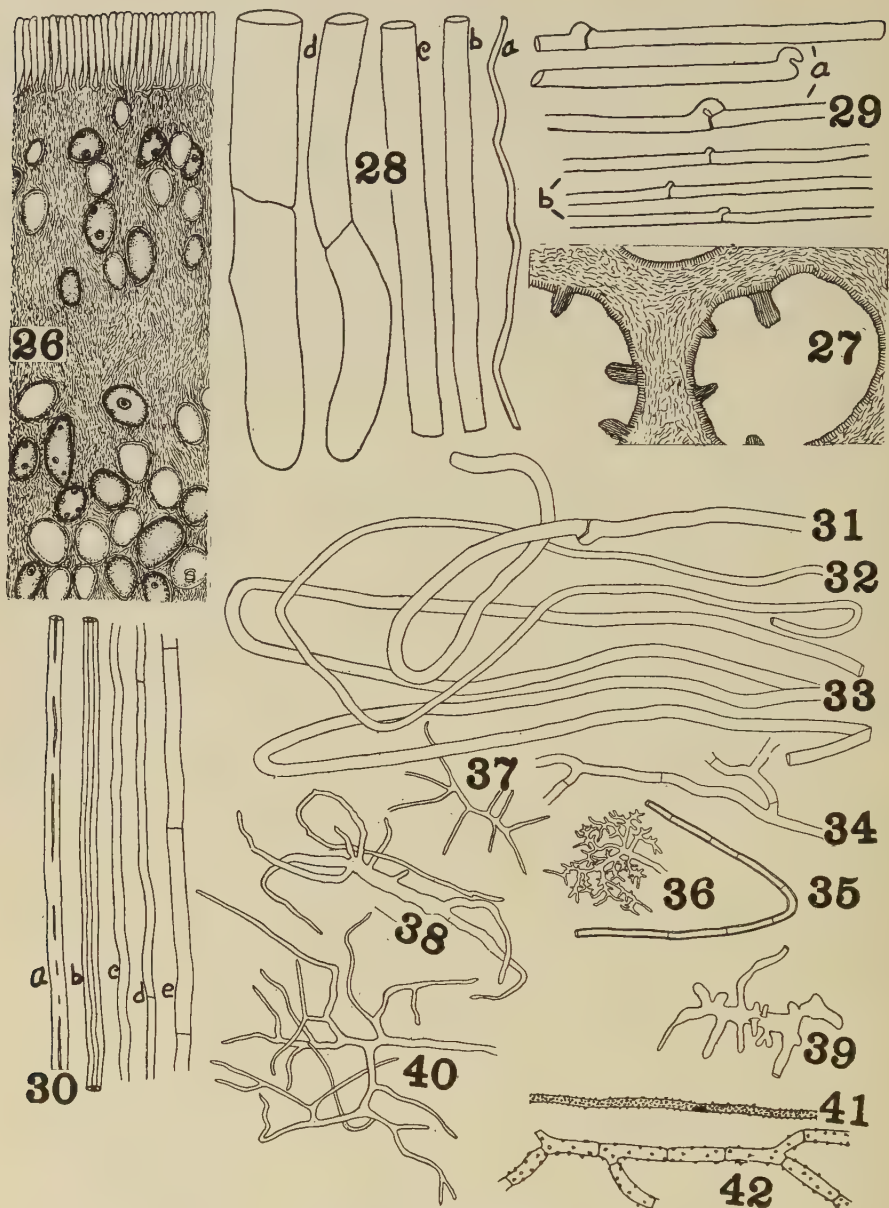
TEXT FIGURES 26–42

Fig. 26. Vertical section of the hymenium and the sub-hymenial region of *Stereum murrayi* showing the abundant imbedded vesicular cells.

Fig. 27. Cross section of the hymenium of *Polyporus maximus* showing abundant hyphal pegs.

Fig. 28. Hyphae to show variations in diameter: (a) of *Poria fimbriata*, 2μ diameter; (b) of *Polyporus versicolor*, 6μ diameter; (c) of *P. zonalis*, 9μ diameter; (d) of *P. obolus*, 12μ and 16μ diameter.

Fig. 29. Hyphae to show clamp connections: (a) of *Polyporus caesius*, the middle one showing the hypha broken at the cross wall, leaving the hook-like clamp; (b) of *Poria mucida* with small clamps drawn to the same scale as (a).

C. Septation. Beginning students in mycology are so often told that lack of septation is a feature characteristic only of the hyphae of Phycomycetes, so that it may actually appear to even more advanced students of the subject that the caption of this paragraph is misleading. While it may very well be that no such things as aseptate hyphae occur in Hymenomycetes, yet it is certainly true that there are many species in which septa are not discernible by the methods recommended in this paper, while they are perfectly apparent and conspicuous in other species. On this basis, then, I venture the assertion that the hyphae of the subiculum (or context) of *Poria subacida* (Fig. 30A), *P. medulla-panis* (Fig. 37), *P. eupora*, *Trametes rigida*, *T. cubensis* (Fig. 30B), and many more species, are aseptate or show no septation with the usual treatment. In others, septations are present but not abundant. In such species as *Poria corticola* (Fig. 30C), *P. ambigua* (Fig. 30D), *P. semitincta*, and others, septa are frequent but not relatively abundant, dividing the hyphae into long cylindrical cells, easily observed under the microscope. This septation is carried further in *P. griseo-alba* than in any other species, resulting there (Fig. 42) in very short cells, highly characteristic for the species. In yet other species, particularly forms with brown context in *Poria*, *Fomes*, and *Polyporus*, septa are never visible in the older brown hyphae, yet are present in the lighter colored ones with which they are admixed.

When these hyphae are examined as to the thickness of the walls it is evident that cross walls are lacking in most cases where the lumen of the hypha is reduced by extra thickness of the inner wall, and this is often carried to the practical or entire occlusion of the lumen. In thin-walled hyphae cross walls are far more likely to be present.

D. Manner and Extent of Branching. While it would obviously be impossible for hyphae to extend without branching from the substratum to their extremities in the fruiting body, yet a great deal of variation as to the extent of branching is prevalent. Here again different species are comparable only when the hyphae are taken from the same general region. It is easily demonstrated that hyphae in

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Fig. 30. Hyphae illustrating cross walls: (a) of *Poria subacida* without septae; (b) of *Trametes cubensis* without septae; (c) of *Poria monticola* without septae; (d) of *P. corticola* with occasional septae; (e) of *P. ambigua* with more numerous septae; compare also figure 42.

Fig. 31. Unbranched hypha of *Polyporus albellus*, 300μ long.

Fig. 32. Unbranched hypha of *Poria subacida*, 510μ long.

Fig. 33. Unbranched hypha of *Polyporus pavonius*, 950μ long.

Fig. 34. Hypha of *Poria ambigua*, sparingly branched.

Fig. 35. Unbranched hypha from the context of *Polyporus taylori*, to be compared with figure 36.

Fig. 36. A hyphal complex from the context of *P. taylori*.

Fig. 37. Considerably branched hypha of *Poria medulla-panis*.

Fig. 38. Hyphal complex from the context of *Polyporus pavonius*, to be compared with figure 33, both from the same mount.

Fig. 39. Hyphal complex of the more irregular type from the context of *Polyporus occidentalis*.

Fig. 40. Hyphal complex from the context of *Polyporus anceps*, showing dichotomous branching.

Fig. 41. Finely incrusted hypha of *Poria subincarnata*.

Fig. 42. Sparingly incrusted hypha of *Poria griseoalba*.

the region of the immediate subhymenium or the trama, giving rise to the basidia, are always extensively branched. But in the context, or those parts of the trama more distant from the basidia, more variation is to be observed.

In a very large number of species one can readily demonstrate two types of hyphae in the context, both being readily discernible in crushed preparations from that region. In most cases one of these types is more or less unbranched (Fig. 35) and the other more or less richly branched (Fig. 36). For this second condition I propose the term "hyphal complexes." I have no doubt that these hyphal complexes have a significance that has not been hinted at up to the present time. They seem to be present in all species of the old *Polystictus* section and are more or less in evidence in many others. Indeed, they may prove to be present in all species, but of this I am not certain. I have seen them, however, in such widely separated species as *Polyporus lucidus*, *P. anceps*, *P. chioneus*, *Trametes cirrifer*, and others. In most cases the ordinary hyphae are of larger diameter, and form as it were, the framework of the tissue involved, while the hyphal complexes are often less conspicuous, the hyphae of narrower diameter or attenuate at the tips. In a few cases the body of hyphae making up the complex originates from a hypha of unusually large diameter, as in the case of *Polyporus pavonius* (Fig. 38) and *P. tsugae*. In others they originate as the termini of hyphae of the usual sort, often dendritically branched to a marked degree, as in *P. anceps* (Fig. 40) and *P. taylori* (Fig. 36). In the *Polystictus* section (Fig. 39) they are often more botryiform, sometimes the secondary hyphae appearing only as bud-like outgrowths along the sides of the parent hypha, giving the entire complex a very characteristic shape.

The ordinary hyphae of the context are often unbranched for lengths that run entirely through a piece that may readily be pulled out with the forceps. They thus may extend well across the field of the low power microscope without branching. Of course even such lengths as these are in reality very short. The longest single strand of mycelium I have ever obtained by the crush method was scarcely 1000μ (1mm.) long, and lengths of 1/6 to 1/4 mm. are more frequent. Long, unbranched hyphae are a constant feature of the subiculum of *Poria subacida* (Fig. 32), of *Polyporus albellus* (Fig. 31), and of the tough and leathery species in the *Polystictus* section (Fig. 33). Yet these ordinary hyphae are often branched, sometimes considerably so, as in *Poria medulla-panis* (Fig. 37) and *Polyporus chioneus*, often only slightly so as in *P. ambigua* (Fig. 34) and many others.

D. Incrustation. Often times the hyphae of the subhymenial region, rarely of the context of pileate species, are incrusted with small crystals, perhaps of calcium oxalate. These may show up in thin sections through the subhymenium but are most easily observed in crushed mounts. There is little variation in this phenomenon where it occurs, and the character has only a limited value. It has been recognized by Burt in the *Thelephoraceae* and I have made use of it in connection with the genus *Poria* (Figs. 41, 42). Otherwise it has received only incidental recognition.

III. Tissue Differentiation

Under this heading I shall discuss that type of differentiation which results in a more or less definite zonation in the structure of various parts of the fructification, but particularly in the subhymenial region of resupinate species and in the context of pileate forms. Material illustrative of these differences is obtained from vertical sections through the fruiting bodies, preferably parallel to the course of the main body of hyphae.

In many fungi no conspicuous differentiation exists. For example, in practically all species of *Poria*, in most species of *Corticium* and *Peniophora*—all resupinate forms— the subhymenial region is homogeneous in structure (though not lacking as some of the older texts state). It may be of a very open structure consisting of loosely interwoven or suberect and practically parallel hyphae. (Figs, 7, 23, and Pl. III, fig. 8); or it may be very compact, of closely intertwined hyphae (Figs. 18, 19, and Pl. I, fig. 1, Pl. IV, figs. 4, 7.). Likewise the context of most species shows no differentiation into zones or layers, though varying in compactness in different species as does the subhymenium. Of course, even these variations may be recognized as of diagnostic value to some extent, since, in the same species, the range is relatively small. However, it is certainly true that observations on these points have not been made in large number, so that inferences and generalities are not safe.

In the context of pileate forms one occasionally meets with arrangements striking enough to be of significance. Usually this takes place either in connection with (a) a gelatinization process of some portion of the context, or (b) in connection with the differentiation of a crust or of a hairy covering. Of the former type may be mentioned *Mycena leaiana*, *Panus angustatus*, and *Pleurotus serotinus*, in each of which there is developed an outer gelatinous layer (Fig. 46, and Pl. IV, Fig. 1), very conspicuous when seen in sectional view under the microscope. Gelatinized tissue is easily recognized, once its salient features are learned, yet difficult to describe in words. The tissue is always light in color and the outer walls of the hyphae become diffluent and merge into each other until the outlines disappear (see also Pl. II, fig. 5). Except in cases of extreme gelatinization verging on liquefaction, such tissue cuts well with a keen razor, particularly when bordered on one side by a firmer layer. Its consistency is, in fact, usually soft-cartilaginous or waxy.

Practically all species of the genus *Stereum*, most of the pileate species of *Hymenochaete*, many of the *Polystictus* types of *Polyporus*, and some species of *Fomes* show differentiation connected with the development of a crust or a hairy covering over the pileus. The differentiation consists in the formation of a very dense narrow zone leading into the more open context tissue on the inner side and differentiating it from the floccose hairy covering or "tomentose layer" on the outside (Pl. IV, fig. 2). The tomentose layer may be only poorly developed, in which case it sooner or later wears away leaving the narrow dark zone as an incrusting surface. Such is the condition in *Fomes pectinatus* and in *Polyporus fruticum* (Pl. IV, fig. 2), where old specimens have a distinct crust, though a tomentose covering is present in young specimens. In the latter species, and

in others, the tomentose outer layer is often many times thicker than the remainder of the context, the two being separated by a narrow dark zone. Probably all species possessing what has been termed a duplex context, that is, soft and spongy above and firmer next the hymenium, are of the same type, the outer soft layer being homologous with the tomentose layer of *F. pectinatus* and *P. fruticum*. The context of *Polyporus iodinus* shows this differentiation remarkably well in sections, where in fact four different zones may be recognized (Pl. IV, fig. 3). The tomentose layer is subtended by the usual dark zone and this in turn is underlaid by a broader light colored zone comprising most of the context, while another darker zone separates the context from the tissue of the tubes. The more typical examples of a hairy covering associated with zonation are seen in the genera *Stereum*, *Hymenochaete* (pileate forms), and some species of thin coriaceous *Polyporus*. Here the dark zone is near the upper surface of the pileus (Pl. IV, figs. 4, 7), but as in the cases cited above, the hairy covering may wear away, (for example, *Stereum fasciatum*, *S. hirsutum*, and *Polyporus (Polystictus) maximus*) exposing the underlying layer that is often hazel or reddish in color. In all of these cases this zonation shows up more conspicuously if the sections are cut parallel to the course of the hyphae, rather than at right angles to them. In the genus *Stereum* the presence of this narrow dark zone is taken by Burt to be characteristic of the genus, and by means of it the species of *Stereum*, even though in resupinate condition, can be separated from the truly resupinate genera *Corticium* and *Peniophora*. This might lead to the conclusion that resupinate conditions of all pileate species in related genera and families might also be separated from truly resupinate species in the same way. But such is not the case, for example, in the genus *Poria*, where such a separation is most needed. Even when such a layer is present I think we cannot safely infer that the species is normally pileate. For example, in *Odontia granulata*, discussed below, the layer is present but I have observed that species over many years and am confident that it does not develop a pileate condition. On the other hand, many pileate species do not develop such a layer either in their normal or in their resupinate condition. As a matter of fact, Burt admits into the genus *Stereum* a few species that do not possess this layer.

In truly resupinate genera layering is often quite evident in the hymenium itself, or in the subhymenial tissue. This may arise purely as an expression of a perennial trait in the fungus, just as the macroscopic appearance of layering in the tubes of a *Fomes* denotes the same. Certain of the thick species of *Corticium*, for example, *C. galactinum* (Pl. IV. fig. 5) and of *Stereum*, (for example, *S. murrayi*) and of *Hymenochaete*, (for example, *H. curtisii* (Fig. 43) appear to illustrate this point, although the annual basidial layers can scarcely be distinguished, and I rely here mainly on observations concerning the duration and the texture to explain the distinct layering that is present.

In other species the layering is evidently not explained by periods of growth. As indicative of this, in *Grandinia granulata* there is present a distinct layer of parallel hyphae next the substratum, and this is separated from the hymenial region by a very loose region of semi-erect hyphae, giving a very characteristic

appearance to the sections (Pl. IV, fig. 6). In resupinate species of *Hymenochaete*, as pointed out by Burt, the subhymenial region may be homogeneous, the subtending hyphal layer bearing the setae as in *H. multisetae* (Pl. II, fig. 4), *H. corrugata* (Fig. 11), and others, where, without regard to the width of this layer, setae arise from all parts of it. In other species the setigerous layer is limited to a zone underlying the hymenium, the remainder of the subtending tissue being free of setae, as in *H. tabacina* (Pl. IV, fig. 7), *H. rubiginosa*, and a number of other species.

Other types of tissue differentiation are not unknown. In a few species, represented by *Polyporus dichrous* and *P. amorphus*, the entire hymenial region is waxy in texture and in section (Pl. IV, fig. 8) shows the characteristic gelatinization of the hyphae in that region. Yet another type of differentiation is shown in the gills of many Agarics, although not enough work has been done to warrant an extended discussion. I have observed, however, that in the gills of *Mycena leaiana* and in several species of *Pholiota* in the group with *P. adiposa*, *P. squarrosoides*, and *P. aurivella*, there is present a central medulla or cylinder of closely intertwined hyphae of small diameter, surrounded by loosely interwoven hyphae leading up to the basidial layer (Fig. 44). In many other species of *Pholiota*, that is, *P. praecox* and its relatives, this medulla is not present.

IV. Crystalline Material

Aside from the incrusting material frequently present on the hyphae of fungi there also occur larger accumulations of inorganic materials in crystalline form. Large irregular crystals are often found imbedded in the tramal tissue of members of the *Polyporaceae* (Pl. IV, fig. 9). I cannot vouch for their diagnostic value, yet their presence should always be recorded for possible cases of comparison. In *Aleurodiscus* of the Thelephoraceae crystalline matter is sometimes present, similar in quantity to that in *Polyporus* (Fig. 45), but in some species in so much greater quantity that the plants have distinctly a calcareous texture when cut. One would expect, however, that the quantity of this material present might vary with the age of the plant, and to verify this point observations should be made on plants at various stages of maturity.

Conclusion

Now, in conclusion, I do not wish to leave the impression that microscopic characters are to be emphasized to the exclusion of macroscopic features; nor on the other hand is it to be thought that microscopic characters, in the Hymenomycetes, are of use only in the isolated genera I have mentioned. Most certainly their proper use is to supplement macroscopic features—not to replace them—and such a legitimate use is justified in any group where contrasting microscopic features are present. By all means, identify on the basis of external appearances where that can be done with certainty, but in cases of doubt, however small, do not hesitate to allow the facts of internal structure to decide the case. External features are but half the story, and many species externally similar are internally very dissimilar, and these dissimilarities, if constant (and

by virtue of their position they are more likely to be constant) are just as indicative of specific differences as are external characters. I plead for a sane use of *all* the morphological characters of a plant—not simply those that are most striking or most easy to detect.

It may be urged by way of objection by those who have had even more than a minimum of mycological training, that only a limited number of students especially trained, can identify our fungi belonging to these difficult groups,
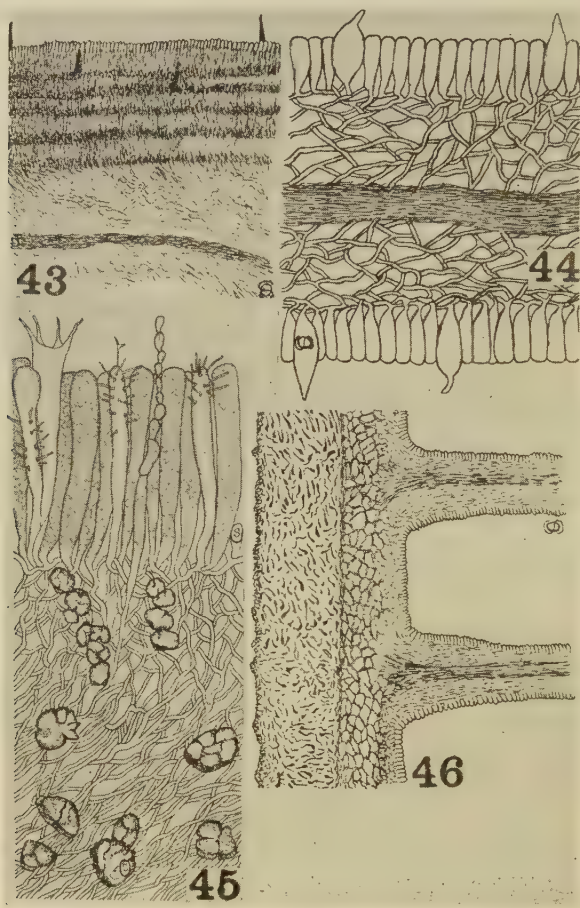
TEXT FIGURES 43–46

Fig. 43. Vertical section through the hymenial region of old specimen of *Hymenochaete curtisii* showing layering probably representing the perennial character of the fungus.

Fig. 44. Cross section of a gill of *Mycena leaiana* showing the central medullary strand of more compact hyphae.

Fig. 45 Vertical section through the hymenium and the subhymenial region of *Aleurodiscus amorphus* showing imbedded crystalline masses.

Fig. 46. Vertical section through the pileus and gills of *Mycena leaiana* showing the well developed gelatinous layer over the pileus; to be compared with Pl. fig. 1.

If that be true then we must make the best of it, for there can be no iota of doubt that it is the only practical method available in some genera and we must hold up work of this sort as a standard of excellence for all groups of like difficulty of approach. But I do not believe it is true. I believe it is possible for anyone with the rudiments of a mycological education to acquire quickly a considerable degree of facility in this direction. Certainly we all agree that no student, regardless of his special line of botanical work, should be allowed to complete his postgraduate work without acquiring some degree of precision in the use of the sectioning knife. The remainder is comparatively simple. We must have, it is true, adequate guide posts in the way of illustrative material to point out the high lights and the shadows, by which I mean the significance of the structures he will meet. In other words, our mycological household must be put in order, and the meaning of the hieroglyphics that some of us have made must not be open to double interpretation. We must stop and define our position, dig ourselves in, as it were, that our students may quickly realize when they have come to the border of "No Man's Land," and with the least possible effort they may take up the work that older eyes and less steady hands are ready to turn over to them. It is for careful painstaking work of this sort that I plead. May the mycologists of the future be able to say with more earnestness perhaps than did a certain European botanist to a young American student to whom he was demonstrating the proper cutting of free-hand sections: "Ach, meine Schnitte sind noch zu dünn."

EXPLANATION OF PLATES

All figures in the plates are photo-micrographs of free-hand sections stained with eosin (in a few cases unstained) and mounted in glycerine.

PLATE I

Fig. 1. Vertical section of the hymenial region of *Stereum umbrinum*, showing brown cystidia.

Fig. 2. Cross section of the hymenial region of *Poria subacida* showing inconspicuous slightly projecting cystidia.

Fig. 3. Vertical section of the hymenial region of *Panus angustatus* showing numerous projecting cystidia.

Fig. 4. Cross section of the hymenium of a species of *Poria* showing abundant but small cystidia.

Fig. 5. Vertical section of the hymenial region of *Odontia granulata* showing a single hypha-like, septate cystidium at the apex of the granule.

Fig. 6. Cross section of the hymenium of *Poria ferruginosa* showing conspicuous setae.

PLATE II

Fig. 1. Crushed material of the context of *Polyporus glomeratus* showing imbedded setae best shown at A but visible also in the denser portion of the material.

Fig. 2. Vertical section through context and hymenium of *Polyporus glomeratus*, showing portions of imbedded setae.

Fig. 3. Cross section of the hymenium of *Poria perennans* showing the imbedded setae as cut crosswise and visible as dark circles.

Fig. 4. Vertical section of the thin fruiting body of *Hymenochaete multisetae* showing abundant setae; for comparison with text figure 14.

Fig. 5. Vertical section through the hymenial region of *Seismosarca alba* showing the abundant flexuous gloeocystidia; for comparison with text figure 16.

Fig. 6. Vertical section through the hymenial region of *Stereum sanguinolentum* showing the dark elongated conducting cells; for comparison with text figure 19.

PLATE III

Fig. 1. Cross section of the hymenium of *Poria vulgaris* showing the abundant narrow organs probably best regarded as paraphyses.

Fig. 2. Vertical section of the hymenium and the subhymenial region of *Stereum murrayi* showing the imbedded vesicular cells; for comparison with text figure 26.

Fig. 3. Vertical section of the sub-hymenial region of *Stereum purpureum*, showing the dark imbedded vesicular bodies; for comparison with text figure 25.

Fig. 4. Vertical section of the hymenium of *Trametes serpens*, showing the projecting hyphal pegs.

Fig. 5. Single hyphal peg of *Trametes serpens*, enlarged.

Fig. 6. Cross section of the hymenium of *Polyporus ectypus* showing a single low-conoidal hyphal peg.

Fig. 7. Cross section of the hymenium of *Polyporus versicolor* showing a single hyphal peg.

Fig. 8. Vertical section through the fruiting body of a species of *Corticium* showing the loose arrangement of the sub-hymenial region.

PLATE IV

Fig. 1. Vertical section through pileus and gills of *Panus angustatus* showing the upper gelatinous layer subtended by a denser context layer; compare with text figure 46.

Fig. 2. Vertical section through pileus and tubes of *Polyporus fruticum* showing the dark narrow zone separating the tomentose layer above from the context layer below.

Fig. 3. Vertical section through pileus and tubes of *Polyporus iodinus* showing a more marked zonation with two well defined layers below the dark zone.

Fig. 4. Vertical section through the pileus of *Stereum hirsutum* showing the dark narrow zone separating a loose tomentose layer from a dense sub-hymenial region.

Fig. 5. Vertical section through the resupinate fruiting body of *Corticium galactinum* showing distinct layering that probably originates from the perennial habit of the fungus.

Fig. 6. Vertical section through the resupinate fruiting body of *Odontia granulata* showing a distinct layer of parallel hyphae next the substratum.

Fig. 7. Vertical section through the pileus of *Hymenochaete tabacina*, showing zonation, the setae confined to a narrow layer bordering the hymenium. On the opposite (lower) side a narrow dark zone separating the tomentose layer from the context tissue (hyphal layer, of Burt).

Fig. 8. Vertical section through the pileus and tubes of *Polyporus dichrous* showing the gelatinization of the entire hymenial region.

Fig. 9. Cross section of the hymenium of *Polyporus pavonius* showing large angular crystals imbedded in the trama.
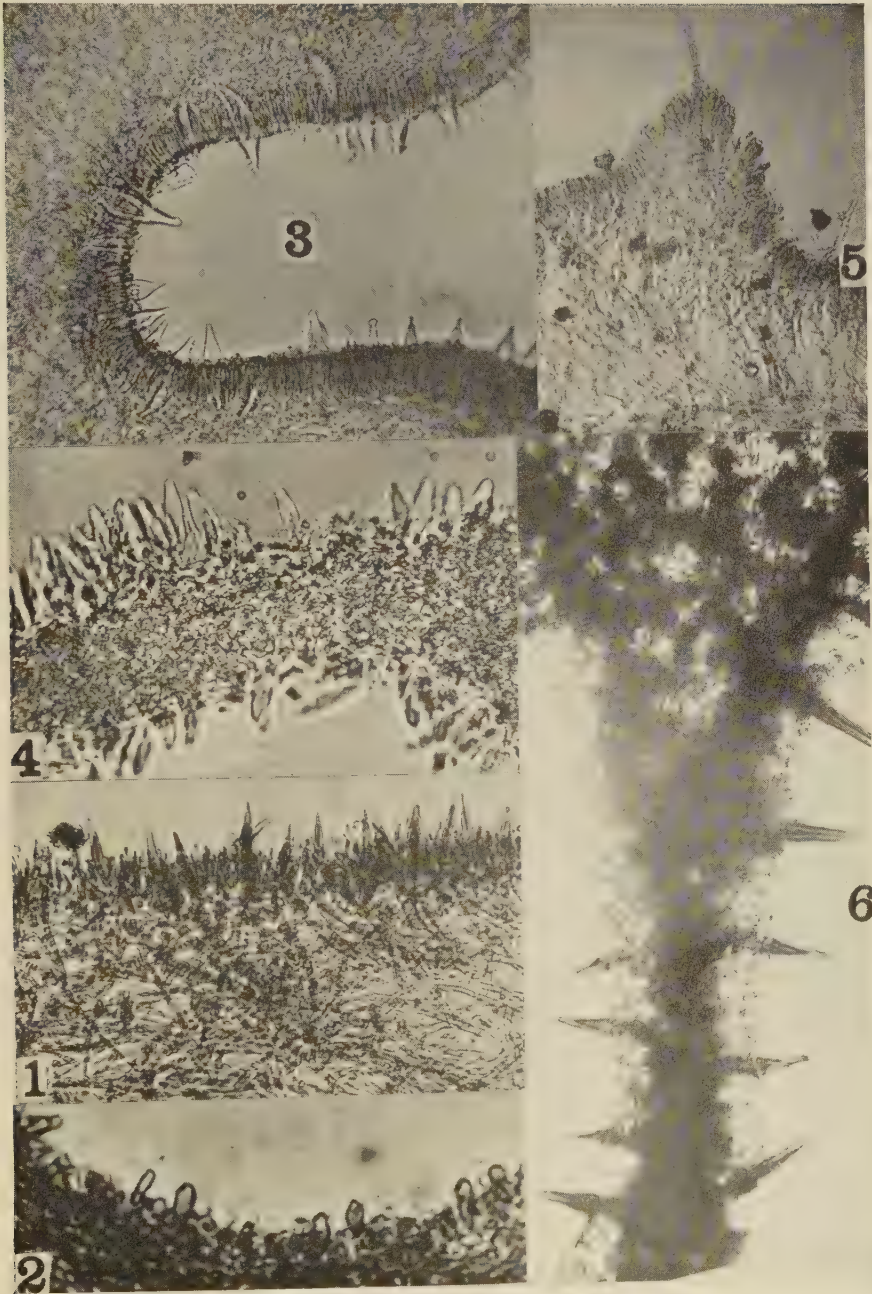
OVERHOLTS: TAXONOMY OF HYMENOMYCETES
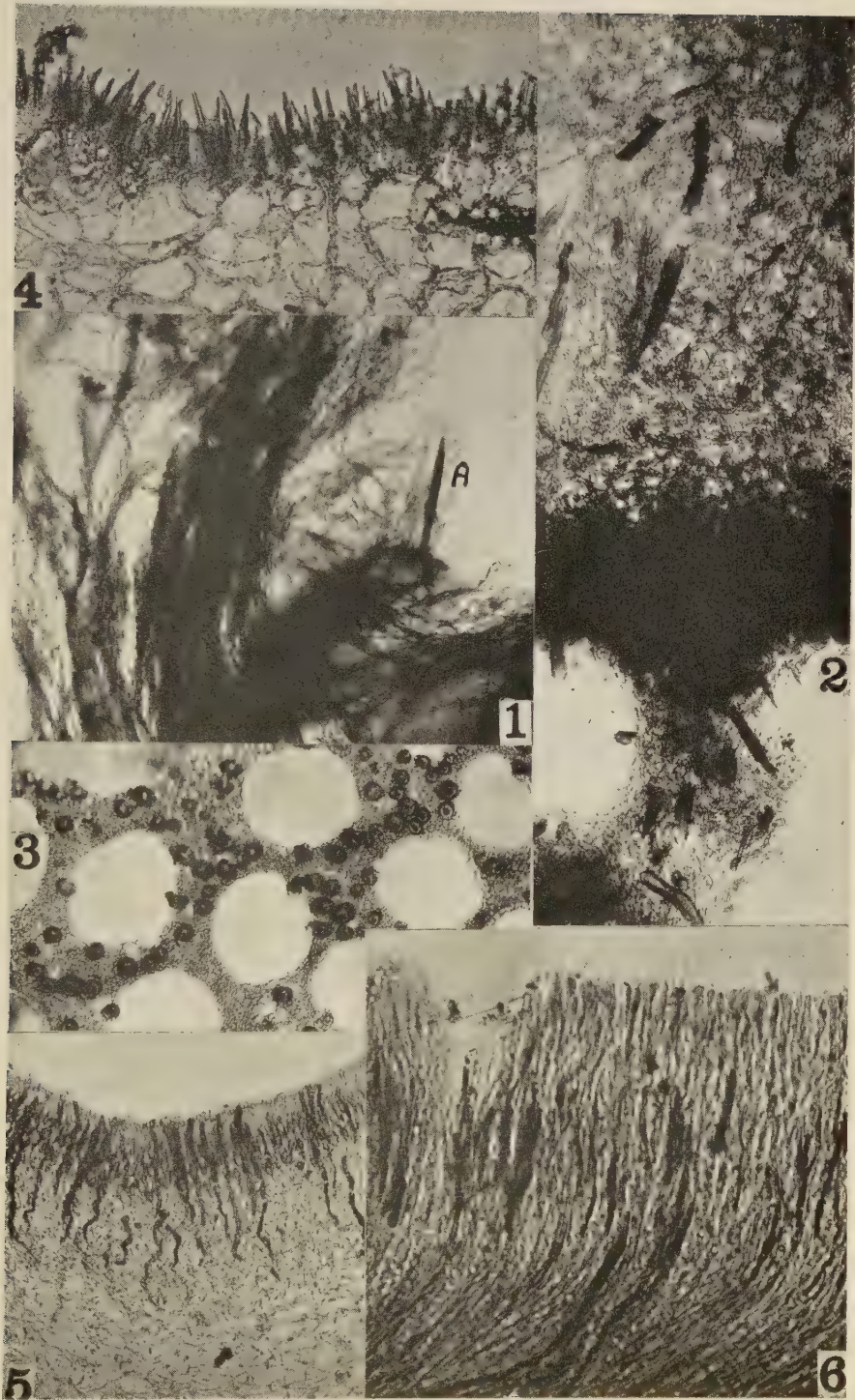
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OVERHOLTS: TAXONOMY OF HYMENOMYCETES

PLATE IV
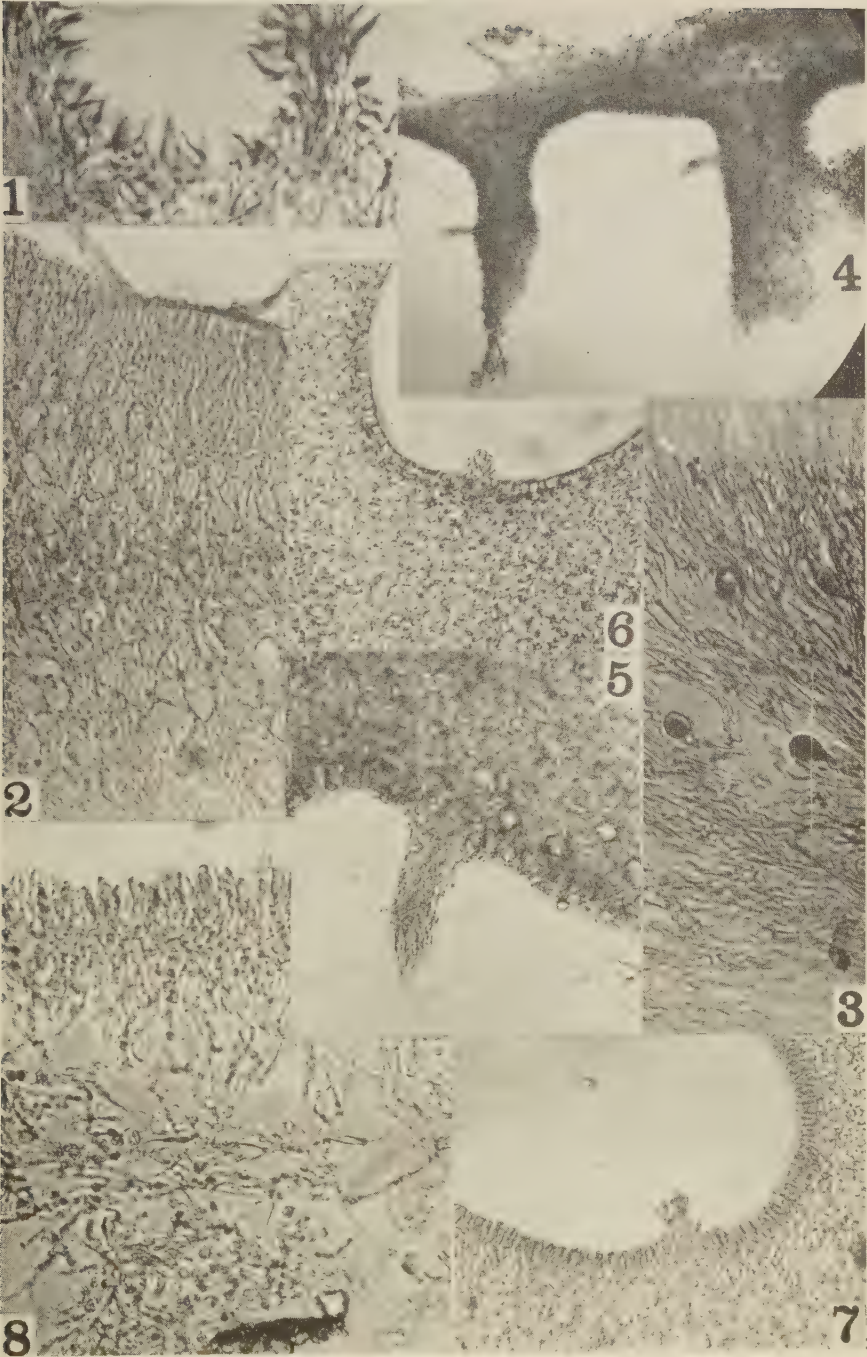
OVERHOLTS: TAXONOMY OF HYMENOMYCETES

A DEFENCE OF THE MORPHOLOGICAL CLASSIFICATION OF FUNGI[1]

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When the writer began his duties as Mycologist to the New Zealand Government, he was faced with the problem of identifying species of fungi causing diseases of plants. Owing to the fact that there was no herbarium available for reference (for no mycological work had previously been undertaken in this country), and to the isolated position of New Zealand, he was forced to take up systematic studies of fungi in addition to plant pathological work. Early in these studies he was confronted with the problem of delimitation of species; for on referring to current literature he found there were two schools of systematists: those who classified fungi according to morphological characters, in conjunction with habitat (herein termed mycologists); the second (here termed pathologists) who classified by the behaviour of the organism toward its host, on culture media, or both. These latter considered morphological characters insufficient or worthless for specific delimitation, and frequently went to the extreme of considering cultural characters alone to be of value for classificatory purposes.

The writer believes most mycologists are agreed that a species is but a group of individuals, separable from other groups placed in the same genus, by the presence of certain characters whereby they may be recognized. In modern systematic works it is customary to provide a key to the species of a genus—an artificial arrangement by which each species may be separated by its major characters. Should it not be possible thus to key a species, then to the mycologist it does not exist.

The mycologist also recognizes the fact that the specific characters change with the genus, a fact only too frequently overlooked by those who would define a species as being a fixed, immutable entity. To each species is applied a label—the specific name—useful in that it provides a ready means of access to literature and herbaria. McLean[2] has ably summarized the position, thus:

"To the present day systematist species are no more than a series of packets into which he sorts objects. About x, the intimate constitution of these objects, he makes neither assumptions nor prophesies; but if $x \times y$ (the environment) $= xy$ (the observed object), he needs only to define the two latter terms as clearly as possible, and, if he can develop quantitative methods of assessment with which to do it, so much the better."

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, Aug. 19, 1926. (Read by Fred J. Seaver).

[2] McLean, R. C. Remarks on the nature and definition of species. Trans. British Mycolog, Soc. **9**: p. 57. 1923.

A systematic publication should then be a work based on morphological characters whereby the species considered therein may be readily recognized. The more systematic (that is, artificial) such a work, and the more convenient its arrangement, the more useful would it be.

Numerous plant pathologists, forced to recognize differences in the behaviour of organisms towards their hosts (differences, which not being morphological, are overlooked by the mycologist) would subdivide the mycologist's species into numerous smaller ones, based on these differences. This biological and cultural classification is more and more being thrust forward, doubtless owing to the fact that the majority of those working with fungi are pathologists, rather than systematists. Further, the modern tendency is for the pathologist to limit his studies to one or several species of a genus, and because of this his outlook is necessarily more limited than that of the mycologist, who works with many genera and species.

Were the pathologist to attempt a biological classification of the fungi of any region, he would find that they would segregate into three main groups: (1) Those readily grown upon culture media; (2) those cultivated only on the living host plant; and (3) those it is not possible to culture by any of the present methods in use.

With the first group the most work has been done, principally because into this group fall the major number of plant pathogens; and it is upon the results of such work (almost entirely with pathogenic species) that criticisms of the morphological classification of species have been lodged.

When one considers how little is known of the media with which the pathologist works, and the highly artificial conditions with which such work is surrounded, it is surprising (to the mycologist) that so much reliance has been placed on such work. For it requires but little change in the composition of media to cause striking changes in the behaviour and structure of most fungi grown thereon, as is evidenced by the recent researches of Brown.[3] Media used in the cultural classification of species, frequently (nay, usually) consist of vegetable decoctions, varying with the conditions under which they are prepared, and the sources from which the materials are obtained.

Specific delimitation, based on cultural characters, would necessitate keeping such "species" in a viable condition, leading to the maintainance of a culture herbarium. This offers no difficulties to institutes where labour and monetary assistance are easy to obtain, but becomes a serious problem in the usual small laboratory. Then, too, there is a tendency with certain pathogens maintained in culture over a period, to lose their pathogenicity; thus those "species" based on biologic behaviour towards their host (for example, exhibiting parasitism) would gradually lose their one "specific" character.

[3] Brown, W. A.   Experiments in the growth of fungi on cultural media.   Ann. Bot. **37:** p. 105.   1923.

—————————Studies in the genus Fusarium.   *Ibid.* **39:** p. 373.   1925.

—————————Study of forms of Fusarium occurring on apple fruit.   Rept. Imperial Botanical Conference p. 339   London, 1924.

Finally, the complicated nature of the technique involved in the delimitation of species by cultural characters, would lead (and has led) to this work being limited to a few specialists, a defect that would become more serious as time passed. That such is a fact is evident in the case of the classification of "species" of the genus *Fusarium*. For, thanks to those few pathologists who have worked with this genus, it is in such a chaotic condition that the writer believes few mycologists or pathologists would undertake the delimitation of any species placed therein.

The second group contains those species which the pathologist is unable to obtain in culture, but is able to grow upon the living host. Such a group is limited to the Uredinales and the Erysiphaceae. As a result of the work of Eriksson[4] upon biologic specialization, considerable confusion exists in literature as to the specific names to be applied to most of the cereal rusts. Not only pathologists, but unfortunately mycologists as well, have accepted as valid many of the biologic "species" proposed by Eriksson; consequently later workers, classifying on morphological characters, have had to use a different terminology, one which is unfamiliar to most pathologists, as is evident by their usage of Eriksson's specific names. Even were the use of biological species permissible, the use of Ericksson's "specific" names is not, for as the writer has shown elsewhere,[5] later workers, using the same species and differential hosts, have obtained results quite different. Stakman and his collaborators[6] have recently shown that 37 biologic forms of *Puccinia graminis* are present in North America. Stakman[7] emphasizes the fact that purity of the host line is essential in this work (a factor completely overlooked by Eriksson) which invalidates the whole of the work of Eriksson and others of his period.

Should specific delimitation of fungi on biologic forms be accepted in the classification of the Uredinales, then these 37 biologic forms must be given specific rank, a matter which would serve no useful purpose, and would only further add to the confusion already existing in the systematics of the species of the cereal rusts.

A second form of biological classification of the Uredinales has recently been published. In "North American Flora," volume 7, *Puccinia* and *Uromyces* are split into several genera, according to the presence (or absence) of different spore forms in the cycle. The question arises, does this classification facilitate diagnosis of species, or in any way assist the mycologist or pathologist in his work? The answer lies in the attitude of mycologists and pathologists throughout the world towards this classification, for almost without exception it has been ignored; even by Dr. Arthur's successor, in his papers on the Uredinales.

[4] Eriksson, J. Ueber die Specialisierung der Parasitismus bei der Getreiderostpilzen. Ber. Deut. Bot. Gesell. **12:** p. 292. 1894.
—————————Neue Studien ueber die Spezialisierung der Grasbewohnenden Kronenrostarten. Archiv. für Bot. **8:** p. 126. 1908.
[5] Cunningham, G. H. Relation of biologic specialization in the taxonomy of the grass rusts. N.Z. Jour. Sci. and Tech. **6**; p. 157. 1923.
[6] Stakman, E. C., and Levine M. N. The determination of biologic forms of Puccinia graminis on Triticum spp. Univ. Minnesota Agr. Exp. Stn. Tech. Bul 8, p. 10. 1922.
[7] Stakman, E. C. The species concept from the point of view of the plant pathologist. Am. Jour. Bot. **10:** p. 243. 1923.

Further, should such a practice become generally accepted, then *Puccinia grami-nis* must be separated into two species, for the cycle of this species differs according to locality. In Europe, the full cycle occurs—aecidia on *Berberis*, uredo—and teleuto-sori on cereals and grasses; whereas in New Zealand, Australia, etc., the aecidium is absent from the cycle as it occurs in nature, the teleutospores accordingly being functionless. Biologically, therefore, two species are extant, which to the mycologist is absurd.

A third form of biological classification has been used in delimiting certain species of fungi. One example must suffice: In the Ustilaginaceae a species found on barley is in literature usually placed under the name *Ustilago nuda;* a second on wheat is named *U. Tritici.* These are usually maintained as distinct species, because of the supposed inability of each to infect the host of the other; yet the writer has shown[8] them to be morphologically identical, and considers them to be but biologic forms (at best) of the same species.

In attempting classification upon cultural characters the pathologist would find himself confronted with a third group of fungi—those which it is not possible to obtain in culture. There exist many fungi the spores of which cannot be germinated under all the usual laboratory conditions; of these the species belonging to the genera of the Lycoperdaceae afford an example. With such, the pathologist would be forced to classify upon morphological characters—for no other means is available.

That the pathologist often has reason for complaint against many of the classifications extant is admitted, for the mycologist of today realizes only too well the errors committed in the past—errors which today fortunately are of rare occurrence. With certain of the older mycologists it was often assumed that a species was new if collected in a foreign country, or found on a different host plant!

Another defect, manifest in many systematic works, is the variable nature of the descriptions given therein. Descriptions of different species, drawn up at different periods, by different workers, were usually incorporated without attempt at comparative description or keying. Consequently such works—of which an example is Saccardo's "Sylloge Fungorum"—are of little value as aids in the identification of species.

Taking into consideration the difficulties in the way of cultural and biological classification of species, it would appear that the mycologist has good reason to continue the established practice of classifying species by morphological characters. He does not feel compelled to cast this aside to adopt a chimera; "An ideal unit, which shall be, like a metre measure, intrinsically invariable wherever found although . . . . its material manifestation may vary circumstantially," as McLean[9] has so ably summarized this hypothetical entity—the biologist's species. Nor does he feel compelled to cast aside the vast amount of systematic literature which has accumulated through the years, nor to discard his herbarium—necessary consequences were biological classification to become generally accepted.

[8] Cunningham, G. H.   Ustilaginaceae, or "smuts", of New Zealand.   Trans. N.Z. Inst. **55**: p. 408.   1924.

[9] McLean, R. C. *l.c.*, p. 48.

The writer believes a solution of the problem would lie in the more concise monographing of species of genera occurring in any one region, redescribing the old species in such a manner that they would be readily recognized, and arranging them on the fundamental basis of systematics—that is, by morphological characters. Were this undertaken, many hundreds of so-called species would necessarily be reduced to synonymy; but if such made easier the recognition of the species of a genus, so much the better. That such morphological works would tend to reconcile the differences between the two schools of workers is evident from Salmon's "Monograph of the Erysiphaceae"[10] a work, which although published 26 years ago, is still the standard for all interested in this family.

It is obviously necessary for pathologists to have some system for labeling biologic forms, cultural forms, etc., but it can only lead to endless confusion if they are elevated to specific rank. Stakman and his collaborators[11] have indicated a better method in their work on the biologic forms of *Puccinia graminis*.

[10] Salmon, E. S. Mem. Torry Bot. Club 9: 292 pp. 1900.
[11] Stakman, E. C. and Levine, M. N. *l.c.*

BASIS FOR A NATURAL CLASSIFICATION OF THE UREDINALES[1]

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A natural classification of any group of plants is designed to show the degree of phylogenetic relationship within the group to the best of available knowledge and logical inference. The success in formulating a classification of this character depends upon the state of knowledge, the successful employment of theories, and also largely upon the selection and evaluation of the diagnostic features employed. The Uredinales, or rusts, have proved a particularly difficult group in which to trace relationships, partly due to the diversity of fruiting structures and partly to a lack of detailed knowledge. The present effort is directed toward assorting the different elements that necessarily enter into the problem. A general statement of the requirements is first made with illustrations drawn from the higher plants, and then these applied to the rusts.

In phanerogamic botany the things we classify are held in mind as distinct entities, and no doubt is entertained regarding the application of the names employed. When we speak of an oak or a sunflower there is nothing equivocal about the objects intended. We may be specific and say *Quercus alba* or *Helianthus annuus* and still there is no disagreement among botanists regarding the objectivity of our conceptions. The first requirement in studying classification, therefore, is a distinct understanding of the individuality of the objects to be classified.

It is also taken for granted that the plants in question do not lose their identity in the scheme of classification by appearing under diverse forms. *Equisetum arvense* is but one sort of plant whether taken in its sterile or its fertile condition. *Lithospermum angustifolium* is a name that applies to a single group of individuals whether in their spring form, upright, with large showy flowers, or in their autumn form, lax and decumbent, with small inconspicuous flowers. It matters not under what form or disguise the individuals manifest themselves, classification takes cognizance of each group of objects as a phylogenetic unit. The second requirement is, therefore, that the diversity of forms within the species be duly recognized as covered by the names employed.

It is furthermore necessary to agree about homologies, both of organs and of the structures arising through their association, whatever the form or external appearance. Thus a root, stem, leaf, stamen or ovule, and each vegetable or reproductive structure, whether in a lily, grass, *Rafflesia*, *Lemna*, or any other plant,

must be appropriately referred to. The misinterpretation of homologies only leads to confusion, and their true status is, therefore, a third requirement.

There are many characters which may be utilized for purposes of diagnostic identification. Some characters are conspicuous, others obscure. Some relate wholly to form or structure, as the shape or texture of leaf or flower, others to adaptive features, such as the period of blooming, and still others to the mode of development, as the evolution of the ovule. From a multiplicity of characters it is necessary to select a comparatively few which are deemed of greatest importance for denoting relationship. The choice and evaluation of characters is, therefore, a fourth requirement.

Every classification is likely to include some groups of individuals that from one cause or another are to be accounted less perfect and autonomous than their relatives. Not only are they less advanced in development, but may have the marks of distinct retrogression. It is agreed that the colorless *Monotropa*, or Indian pipe, is a more degenerate form than any *Pyrola*, or other green plant to which it may be related. In general, parasitic and chlorophylless plants show indications of retrogressive development in one or more directions, and this factor must be taken into account in their systematic study. It is necessary to bear in mind, therefore, the kind and extent of degeneration present as a fifth requirement.

The systematist would not get far in arranging his phylogenetic scheme if he did not decide by means of geological data or assumptions from structure which were the more primitive and which the more recent forms among those with which he deals. He may even find it helpful to theorize as to ancestral forms. In any study for a natural classification a broad basis regarding ancestry must be formulated or assumed, and this theoretical feature may be taken as a sixth requirement.

These several underlying features of every effort to solve the relationship of plants, and to classify them accordingly, are rarely formulated. They appear so self-evident that any specific statement seems unnecessary. This is doubtless true in the case of most groups of plants, especially the higher forms, but when we come to the rusts there are some manifestations in their mode of development that do not readily harmonize with the interpretations derived from other groups of plants, and consequently there has been great diversity in the attempts at their phylogenetic arrangement. An important part of the difficulty, the writer ventures to say, is due to the lack of a clear understanding of the ontogenetic process in the rusts and the significance of the different spore-forms.

The rusts are a remarkably homogeneous group. There are few outlying forms, and almost no intermediate forms to connect them with adjacent groups. They are often called the lower Basidiomycetes, but the relationship between the Basidiomycetes and the Uredinales is so remote, and their corresponding features so in need of explanation, that the rusts are best treated as a unique group up to the point where a study is made of their primitive derivation. The present discussion, therefore, will be exclusively confined to the requirements in the assortment of species, genera, and the higher groups within the order of the Uredinales.

1. The unit of classification is the species. Let us test our knowledge of spe-

cies among the rusts. The name of the stem rust of cereals and grasses, *Puccinia graminis*, conveys a fairly clear conception. It is recognized as applying to a rust with definite characters, having one of its stages on the barberry. It is known to have smaller spores when growing on *Agrostis* and some other hard-stemmed grasses, and in its selective preference for hosts is more or less separable into races or strains. The name *Puccinia graminis* may, however, be said to convey as definite conception of a species as does *Helianthus* annuus or *Quercus alba*.

Let us take, as our next example, the equally common leaf rust of cereals and grasses, for which we will assume the name to be *Puccinia rubigo-vera*. When it grows on wheat it is usually called *Puccinia triticina*, for which the alternate stage has recently been shown to occur on *Thalictrum*. When it grows on rye it bears the name of *Puccinia dispersa*, or possibly some other, and has its alternate stage on *Lycopsis;* when on *Elymus*, or other wild grasses in the eastern United States, it may have its alternate stage on *Impatiens*, or on the same hosts in the west, on *Berberis*. Beside the segregations that can be made based on relation to alternate hosts, not all of which have been mentioned, there are an indefinite number of races and strains. It is evident that the species concept in the second example is by no means so definite as in the first example. This difference is partly due to a lack of knowledge regarding the boundaries and variations of the two species, and partly to a lack of agreement regarding the application of the term species among the rusts.

Let us take a third example, that of *Puccinia mesneriana*. This name is applied to a rust on *Rhamnus*, having no aecial or uredinial stages, and with so little variation in its form and appearance that no difference of opinion exists regarding the identity of the species. Both this species and *Puccinia graminis*, while entirely unlike, clearly meet the first requirement of a definite individuality, while *Puccinia rubigo-vera* and many species whose specific boundaries or full life cycles are in doubt must be cited in classification with caution.

2. About one hundred years ago a lively controversy was in progress between those who regarded the rusts placed at that time under the genus *Uredo* as autonomous and distinct species and those who regarded them as only one stage in the development of a *Puccinia* or *Phragmidium*. It finally came to pass, as in the portentious dream of Pharaoh regarding the thin and ill-favored ears on one stalk and the good and full ones on another, that the latter devoured the former, and afterward "it could not be known that they had eaten them," the *Uredo* disappeared and there only remained the genera *Puccinia* and *Phragmidium*. About fifty years later quite a similar ingestion took place. The genus *Aecidium*, with a number of its generic kin, was absorbed by the same "good and full" genera, *Puccinia, Phragmidium, et alii*.

These two episodes in the history of the rusts made prominent the fact, not before recognized, that a species among these plants may appear in two or three highly diverse forms, although it was also ascertained at about the same time that certain species did not go through such transformations. In phanerogamic botany the name applied to a plant, even though a part only was known at the time of

naming, for example, merely the leaves, or flowers, or fruit, becomes the name of the whole plant whenever the remainder of the forms in its life cycle are brought to life. It would seem logical that the same rule should apply among cryptogamic plants. So far as the rusts are concerned, no valid reason has yet been advanced to show that it is not applicable, although arbitrary legislation has undertaken to rule adversely.

Although there may be some question regarding the procedure in selecting an acceptable name for a species, when more than one has been employed, yet there can be no question but that a species should bear only one name and that the name should cover every phase in the full life-cycle, however diversified. Conversely, a species is not fully accounted for, or its true character made evident, unless it is understood how many and what phases the name covers. Thus, *Puccinia graminis* is a name acceptable for the purposes of classification, as it connotes an organism having aecia, uredinia and telia in its life-cycle, while the apparently similar *Puccinia antirrhini* is not a comparable species, because its full life-cycle is not known, and aecia may or may not belong with it. Again, and for the same reasons, *Puccinia malvacearum* is acceptable for the one-phase species, while *Puccinia prostii*, on tulips in southern Europe, is not, because only teliospores are known, indicating a fragmentary cycle. For purposes of classification, therefore, the names of species should be understood to cover the transformations of full life-cycles, unless statement is made to the contrary.

3. The rusts are microfungi, and in their intimate study a microscope is needed. Three classes of results can be obtained with the microscope according to the methods employed. They depend somewhat upon the magnification of the instrument, but much more upon the definition and technical methods. (a) Under lower powers and simple manipulation it is possible to interpret the gross appearance of most rusts. In this way the different forms of sori and spores can be distinguished, and also the parts of a sorus: the peridium, paraphyses, hymenium, and sporiferous layer. (b) Somewhat greater refinement in manipulation and the use of simple reagents will bring out more details, as the thickness, roughness, and pits in the spore walls, the plectenchyma and other parts of a young sorus, and the origin and relationship of the cells composing the peridium, paraphyses, and spore mass. (c) Still greater refinement both in handling the instrument and preparation of material is required to follow the development of the mycelium and sorus cell by cell, the behavior of the nuclei, and the presence and movement of chromosomes and other cellular inclusions.

The introduction of these three methods of study roughly coincides with three periods of advancement and interpretation in the history of the group, although all are still employed and found useful. We are now in the beginning of the cytological period, with only a moderate amount of the rich stores of knowledge awaiting the investigator brought to light. At each period the homologies have been differently understood, but with gradual progress toward a satisfactory interpretation. The limits of the present paper do not permit the discussion of opinions advanced by even the leading writers at different times. No general agreement has

yet been reached. It may not be presumptuous under the circumstances, therefore, for the writer to state in a somewhat dogmatic fashion what he believes to be the best statement regarding the principal homologies among the rusts that the present state of knowledge permits.

All species of rusts are either long-cycle or short-cycle and possess an alternation of generations. In long-cycle rusts, the gametophytic and sporophytic mycelium is discontinuous, and arises independently from the germination of a spore. In short-cycle rusts the sporophytic mycelium is omitted and that stage is consequently greatly abbreviated.

All sori have fundamentally the same structure, developed from a homogeneous primordium, and consisting of a hymenium, sporiferous layer, and protective parts more or less elaborate. There are five kinds of sori: pycnia, aecia, uredinia, telia, and microtelia. The pycnia have the appearance of functionless male organs, and the pycniospores exhibit no true germination. The other four kinds of sori are genuine reproductive structures, and are all of a more or less conidial nature. They present diverse forms and have received various names that are often misleading as to their true character. In all four kinds the spores consist of one or more cells, in every case and they are produced singly when borne on a pedicel, or in chains when the pedicel is rudimentary or obsolete. Under typical development cell fusion in pairs takes place to form the spore-initial cells of the hymenium in aecia and microtelia, but not in uredinia and telia. In long-cycle rusts the aecia and telia are essential organs for the life of the species, one initiating and the other completing the substitute sexual process. The uredinia are solely for asexual multiplication, and are unessential in the individual cycle of development. In short-cycle rusts the aecial and telial functions are united in the same sorus, and there is no organ corresponding to the uredinium.

Besides the four kinds of sori and their spores each species of rust, whether long or short-cycle, also produce basidiospores, not borne in a sorus but on a special organ, the basidium.

Some such understanding of the life history of all rusts must be at the basis of any serious attempt to untangle the threads of relationship. Individual development is naturally expected to represent that of the components of a species, and species with certain like characteristics make up a genus. We shall be groping in the dark if, for instance, we undertake to assort species without knowing if they are long-cycle or short-cycle. It will be disastrous to assemble species without considering the number and kind of their sori. It will not do to assume that aecia must have a certain definite external appearance, like the usual conception of an *Aecidium* for instance, and to deny that they may look like the ordinary conception of a *Uredo*. It will not do to assume that if a microtelium looks like an *Aecidium*, it is therefore an aecium, as in the case of some species of *Endophyllum*. In general, a natural classification must be based upon a recognition of the fundamental character of the organs and the course of development in each species, whatever disguises may be encountered.

4. The most important characters, at least those to be first considered in every

scheme of classification to show relationship, are those connected directly or in-
directly with sexuality. No generally accepted statement can be made regarding
the sexual nature of the rusts, but there are substantial reasons to consider that a
sexual influence begins in the production of aeciospores and terminates in the ma-
turing of teliospores. In this extended sexual process the two fruiting structures
most concerned are the aecium and telium, and in classification the two are almost of
equal importance. The uredinium supplies characters of secondary importance
and is a structure peculiarly susceptible to environmental and host influences, while
the pycnium is of still less significance in this connection. Characters of yet minor
importance in showing broad relationships are those derived from protective parts,
such as the peridium, paraphyses, etc., from adaptive features, for example, the
surface markings of the spores, which are presumably related to means of disper-
sion, and the degree of degeneration as shown by the disappearance of uredinia
and the assumption of a short-cycle condition.

In a very general way it may be stated that the relationships between genera and
the higher groups are most distinctly shown by a combination of characters drawn
from the telia, aecia, and pycnia in which the relative value of the three organs is
in the order named. One may be permitted to look upon these three organs as
bearing in some respects the imprint of sexuality and in a very imperfect manner
corresponding to the flower and fruit of phanerogamous plants.

The relationship between species on the other hand is brought out by the more
vegetative and adaptive features, as indicated above.

5. Retrogressive development implies the loss of structure or function once
possessed by the organism. The deviation from typical forms, however, may in-
dicate either progressive or retrogressive development, and it is often difficult to
determine which of the two it is. As the rusts are chlorophylless and strictly para-
sitic, two influential conditions to induce degeneration, yet their evolution has not
been wholly retrogressive, as may be readily inferred from their multiplicity of
forms, diversity of spores, and numerous species and genera.

The possession of the dikaryon in the gametophytic stage appears to be typical
for the rusts, and we may safely assume, therefore, that uninucleate races have
come into existence through retrogression. As another instance, the suppression
of uredinia, as in the genera *Calyptospora* and *Gymnosporangium*, may be con-
sidered retrogressive, although it does not follow that these genera as a whole are
inferior to related genera possessing uredinia. Some features of an organism may
be advancing at the same time that others are regressive. To cite one more illustra-
tion or retrogression, there are many reasons to believe that the curtailment of the
life cycle by the omission of the gametophytic mycelium, thus producing a short-
cycle rust, is a genuine case of retrogressive development.

6. The advancement of scientific knowledge is greatly enhanced by the employ-
ment of theories. They supply the scaffolding which permits a more speedy erection
of the edifice of facts. Among the rusts they serve an important purpose in
arranging a natural classification. The origin and phylogenetic progress of the rusts
must be largely or wholly conjectural. The available geological data is scant, and

not wholly reliable. Some assumption as to earlier and derivative forms is not only helpful but inevitable, in order to arrange the genera and other groups in any scheme in which an attempt is made to indicate relationship. The more extensively and completely such theories are developed, the clearer will be the grounds for the classification adopted, as well as the need for investigation here and there to substantiate or disprove them.

Some of the specially helpful theories at the present time appear to be that the rusts have developed *pari passu* with their hosts, and that the hosts showing the oldest lineage are likely to harbor rusts also with the oldest lineage. If the assumption is made that primitive, but fully developed rusts, possessed all spore forms, then the short-cycle rusts are more recent, or *vice versa*. The possession of sessile teliospores in compact layers associated with aecia enclosed in a peridium is indicative of early ancestry. A great number of closely related or intergrading forms in a genus points to a more recent origin of the genus than fewer and more fixed species.

Having outlined the six preeminent requirements for developing a natural classification of the rusts it would be interesting to test their application in a tentative scheme, but that would be exceeding the purpose of this paper. It will not be out of place, however, to point out a few examples in which one or more of these requirements has not been recognized.

The place assigned to *Endophyllum* in most, if not all, schemes overlooks true homologies, and assumes an improbable theory of descent. Using the paraphyses and other accessory parts of the uredinia as the chief basis for certain genera, as Léveillé did in founding *Lecythea, Physonema*, and *Podosporium*, gave too much prominence to these organs of secondary value. The use of such genera as *Aecidium, Roestelia, Uredo,* etc., has long been omitted in schemes of classification, because they do not represent full life cycles, but only certain stages, and yet the genera *Puccinia, Uromyces,* etc., have many species assigned to them which likewise represent only stages in development and not full life cycles, and in so far they are only form genera. The absence of uredinia, as well as the short-cycle condition, are doubtless unsatisfactory reasons for the segregation of genera, as done in the writer's account of the North American Flora, except in cases where there are other striking morphological characters, as in the genera *Gymnosporangium* and *Pucciniosira*.

In naming the factors that the writer considers most fundamental as a basis for a natural classification of the rusts it is realized that their successful application depends in a measure upon the amount of available knowledge. Only a few kinds of rusts have yet been investigated with much fulness. The life histories of many outlying species are wholly unknown. The advance in knowledge during the next few years regarding cytology, morphology, physiology and transformations of representative species is likely to exceed that heretofore realized. It is believed, however, that to attain the best approximation to a phylogenetic arrangement of the group the six requirements set forth above most be met, namely: (1) Clear understanding of specific individuality; (2) recognition of diversity of forms within the species; (3) correct interpretation of homologies; (4) evaluation of characters; (5) extent of retrograde development; and (6) theory regarding ancestry.

RESEARCH IN THE BIOLOGY OF ASCOMYCETES[1]

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I will speak on my investigations in the biology of Ascomycetes, although I cannot pretend to be a specialist in this difficult group of fungi. As perhaps you know, I began my mycological research with the blister-rust of the white pine, which has become so dangerous to American forests. Having cleared up the heteroecism of this fungus, I proceeded to investigations of the life history of other Uredineae, later to pathological questions, and finally to studies in the biology of Ascomycetes. I intended to apply the methods found satisfactory in the culture of Uredineae to the investigation of Ascomycetes and Fungi Imperfecti. The study of the connections which exist between the different stages and spore-forms of these fungi, corresponding to the same task in the Uredineae, is one of the most stimulating problems in mycology and, at the same time, on account of its great bearing on phytopathology, is one of the most important ones.

Exact knowledge in this difficult field has been heretofore slight. In the years 1861 to 1865 the Tulasne brothers published their excellent work "Selecta Fungorum Carpologia," in which they describe in Latin what they had been able to learn concerning the development of a large number of fungi, especially Ascomycetes, and illustrated them with wonderful drawings. To mention one example, the life history of the fungus of ergot, *Claviceps purpurea,* was cleared up quite exactly, and Tulasne's beautiful drawings, not yet surpassed, have been reproduced in all text books of botany. But the methods of the Tulasnes were still imperfect. They described and figured what they found growing together on the same substratum, and false combinations, therefore, were unavoidable.

It was A. DeBary, who introduced the experimental methods of culture and infection into the investigation of fungi. Every botanist knows of the famous discovery of the connection of barberry rust with the black rust of cereals, founded upon his preceding experiments on the germination of spores in Uredineae and other fungi. DeBary did not use pure cultures on artificial media for his research since it is not possible in the cultures of Uredineae and Peronosporaceae, and the lack of this method explains a combination of his which seems to be erroneous. It was his opinion that *Botrytis cinerea* is the conidial stage of *Sclerotinia Fuckeliana.* This combination has not been verified by other authors except by Frank and by Istvanffy, both of whom, it seems to me, worked in an insufficiently exact manner. All that we know of the conidia of *Sclerotinia* from the work of Woronin, the celebrated

1725

Russian scholar and collaborator of DeBary, and others, shows them to be so different from those of *Botrytis*, that the combination can hardly be correct.

The method of pure cultures on artificial media was introduced into mycology by Oscar Brefeld. It is superfluous to emphasize the value of Brefeld's investigations. His best work was done in the study of moulds and especially in smuts. But in his investigations on the higher Ascomycetes there is a certain one-sidedness. He generally started his cultures from ascospores, he describes and figures the conidia obtained in these cultures, but only in rare cases did he determine the names of these conidial stages or their position in the system of the imperfect fungi. Moreover, he refused to use the microtome. For these reasons the progress in systematical mycology, especially in the knowledge of the imperfect fungi, is not so great as it might have been.

Many attempts have been made by systematists in mycology, around 1870 by Fuckel, in modern times by von Höhnel and others, to combine ascigerous and conidial forms. There is an abundance of suggested combinations. Many of them, no doubt, are correct, but the greater part consists of conjectures only, exact proof is missing in almost all cases, and it is hardly possible to separate the grain from the chaff. Much more valuable are the scattered investigations (experimental and cultural) on single fungi, on which, in recent years, American mycologists have taken a prominent part. Cultural work in fungi is difficult and is not always successful. Progress therefore can only be slow.

Turning now to my own investigations, I will repeat that starting from the Uredineae I began my work with parasitic fungi. There is a great number of conidial stages living on the leaves of various plants and causing leaf spots. Very little is known about their life-cycles. The problem to be solved has been to find their ascospore stages and to prove the connections. I think it will be of interest to tell something about the methods employed.

The first problem is to get ascigerous stages. We do not know even now a means of producing them with certainty. If we did, the problems of the imperfect fungi might be solved in a short time. In nature, in many cases ascigerous fruit bodies appear in the early spring on the dead leaves or other plant parts which bore conidia the preceding autumn. When they do, it is possible to get them by artificial overwintering. I have been accustomed to collect leaves or stalks, which bear conidia, in autumn and overwinter them in the open air in large flower pots, or in linen bags or in some other manner permitting one to expose them to all influences of weather without loss of material. Judging from experiments with teleutospores of Uredinia and from some experiments with Ascomycetes, alternate wetting and drying seems to have a stimulating and accelerating effect on the ripening of the ascospore fruits, while the cold of winter seems to be without influence. In rare cases perithecia have been obtained in culture on agar or other artificial media. In this way, for instance, Miss B. Stoneman and other American mycologists obtained the perithecia now called *Glomerella* in culture from *Gloeosporium*. I myself obtained perithecia but without contents, in cultures of a *Cephalosporium* from young fruits of cucumbers. Afterward, I found ripe perithecia on shriveled

young fruits in the greenhouse. I cannot give the specific name, because I have not yet determined and figured the form.

Usually ripe ascigerous fruit bodies may be induced to discharge their spores, when they are exposed to dry air after having been soaked in water. If the fungus seems to be a parasite, infection experiments can be made in the simplest and most natural manner by spreading out on a piece of wire-net, which has been fixed over the host plant, parts of the material from which spores are being ejected. If it seems necessary, small pieces of cover glasses may be put on the leaves of the host plant to determine by microscopical examination whether spores have fallen down on the leaves. If the spores are not discharged, or if the fruit bodies are so few that discharge cannot be controlled, or if several different species are present in the same material, it becomes necessary to isolate the fruit bodies and to transfer the spores in a capillary tube or in some other suitable manner. This is sometimes a very difficult task. After inoculation the plants should be covered with a bell jar for a time.

For getting pure cultures on agar I worked out my own method. A moist chamber is made from an ordinary slide, a smaller and thicker slide with a circular perforation (15 mm. diameter) and a cover glass, everything being sterilized. The cover glass is fixed over the perforation by melting wax (from a burning wax-taper used like a brush), and a drop of agar is spread on the inner side of the cover glass. After inoculation the thicker slide is fixed to the thinner one by a drop of water and the whole is placed under a bell glass and kept moist. Inoculation may be effected by causing fruit bodies to eject their spores upon the agar or by transferring spores or conidia from the material or from a suspension in water by a platinum wire or a needle. Microscopical examination is possible as often as desirable and can be continued for days and even for weeks without danger of contamination by foreign fungi.

It is especially valuable that by this contrivance it is possible to follow the development of the mycelium from the spore step by step, that in many cases the formation of conidia may be seen on the very hyphae grown from the spore, and that thus a single preparation is sometimes found to be sufficient to show the connection between an ascigerous fruit and the conidial fungus.

Cultures in tubes or in petri dishes may be obtained by transferring to other media small parts of the mycelium grown on the cover glass. They are useful in proving the identity of a mycelium grown from ascospores with that grown from conidia. They may also be used, in many cases, to provide sufficient quantities of conidia in pure culture for inoculation experiments. For this task great care, much patience, and a severely critical attitude are indispensable. For obtaining good preparations and drawings of the fruit bodies and of the distribution of the hyphae in the diseased tissues, paraffin imbedding and microtome sections are in most cases necessary.

Now let me discuss some of the results of my investigations. A number of rather different conidial fungi were found to belong to the large genus *Mycosphae-rella.* They have been grouped in different genera in the system of Saccardo.

First consider *Septoria* and *Phleospora*. I announced this connection for *Septoria piricola, S. ribis, S. aesculicola,* and *Phleospora ulmi.* *Septoria* and *Phleospora* are closely related genera. The conidia are almost alike. The pycnidial wall enclosing the conidial layer, present in *Septoria* (and one of the characters of this type) but absent in *Phleospora,* is also missing in young stages of *Septoria,* for instance in *S. aesculicola.* Dr. Laibach, of Frankfurt, has added two other connections of *Septoria* and *Mycosphaerella, S. sorbi* and *S. aceris.* Notwithstanding this, it would be false to conclude that all Septorias or Pleosporas belong to *Mycosphaerella.* The ascospores of *Septoria rosae,* which better perhaps may be called *Phleospora rosae,* are thread-like and four-celled, and the fungus, similar to *Mycosphaerella* otherwise, must be determined as *Sphaerulina* (typ. *Rehmiana*), although it is quite different from *Sphaerulina intermixta,* which according to Brefeld, produces a sort of *Dematium pullulans* in culture.

Therefore, not too much stress is to be laid upon the number of cells in the spores or the conidia. There are other Septorias, which do not produce ascospore fruits after overwintering, for example, *S. apii, S. lycopersici, S. scabiosicola.* Have they lost the power to produce ascospores, or did they never possess it, or were the conditions unfavorable, in the experiments? The question remains unsettled.

A third genus of conidial fungi related to *Mycosphaerella* is *Ramularia.* It belongs to quite another class of the Saccardo system, the conidia not being united in layers, and peridial structures being entirely absent. I succeeded in proving the connection already suspected by the Tulasnes, of the well known fungus of the spot disease of strawberries, *Ramularia tulasnei,* with *Mycosphaerella fragariae,* and that of *Ramularia hieracii* with *Mycosphaerella hieracii.* While these fungi are parasitic, *Mycosphaerella punctiformis,* with perithecia very common in spring on dead leaves of linden, oak, and other trees, does not infect living leaves, but produces *Ramularia* in agar cultures as well as on inoculated leaves which have begun to wither. Here in spring they are followed by the *Mycosphaerella.*

A fourth conidial genus, connected with *Mycosphaerella,* is *Cercospora.* The connection was proved for *Cercospora microsora,* a fungus causing black spots on the leaves of linden.

A fifth conidial genus belonging to *Mycosphaerella* is, according to Dr. Laibach, *Ovularia.*

These five groups of conidial fungi being very different, it is convenient to divide the large genus *Mycosphaerella* on the basis of the conidial stages. The sections Septoriosphaerella, Ramularisphaerella, Cercosphaerella and Ovusphaerella may be distinguished. Systematists, perhaps, will not accept this division, because these groups can now be distinguished only by culture, not by morphological characters, and because therefore the numerous other species of *Mycosphaerella* cannot now be distributed among these groups. But there can be no doubt that a *Mycosphaerella* producing a *Septoria,* and a *Mycosphaerella* producing a *Ramularia* are very different fungi.

A peculiarity not yet mentioned of some species of *Mycosphaerella* is, that under certain conditions microconidia having the shape and size of bacteria are formed.

In the beginning I thought they might be contaminations, but in *Mycosphaerella cippocastani* I saw them filling the pycnidia, sometimes mixed with the macroconidia of *Septoria* and originating from the same hymenium; and in pure culture on agar I saw them developing with *Septoria*—conidia from the same hyphae. Therefore, there can be no doubt that they are indeed a second conidial state of these fungi. But they seem to have lost the power of germination. In nature they seem to occur sometimes in fruit bodies resembling those of *Phyllosticta*.

I have not mentioned the connection between *Ascochyta pisi* and *Mycosphaerella pinodes* announced by Atkinson and Stone, because I regard this fungus as a *Didymella*. I indeed succeeded in proving that a *Didymella* is the ascigerous stage of a fungus which causes a very dangerous disease of tomatoes. It produces one-celled and two-celled conidia in the same pycnidia and therefore may be called *Ascochyta* as well as *Diplodina*. *Didymella* is similar to *Mycosphaerella*, but differs in that the asci arise from the whole base of the perithecium and have paraphyses between them, and it seems to me that both characters are present in the photograph in Stone's paper. Grossenbacher's *Mycosphaerella citrullina* also seems to be very near to *Didymella lycopersici*.

I think this falls in another group of connections, that between *Didymella*, an Ascomycete, and *Ascochyta* or *Diplodina* the conidial fungus.

According to Lindau (in Engler und Prantl, "Die Natürliche Pflanzenfamilien") *Didymella* is classed in the Pleosporaceae. In this family connection of ascospores and conidia have been shown in the genus *Venturia* by Aderhold and in *Pleospora* by Gibelli and Griffini. These connections may easily be confirmed by sowing ascospores on nutrient agar. It is remarkable that the two investigated species of *Pleospora*, *Pl. sarcinulae* and *Pl. alternariae* although very similar to each other, produce rather different conidia, *Macrosporium sarcinula* and *Alternaria tenuis*.

Some remarks may be added here on the ascigerous stage of *Heterosporium gracile*, an attractive fungus causing a spot disease on leaves of iris. I got it on the overwintered flower stalks and proved the connection by inoculation experiments and pure cultures. It must be placed in the genus *Didymellina* created by von Höhnel. The name *Didymellina* is misleading, because the fungus differs greatly from *Didymella* in lacking paraphyses, in the thick-walled, irregular shaped asci, their small number and other characters. I called it *Didymellina macrospora*, the spores being very large, about 50 μ long. There is still another species on iris, *Didymellina iridis,* described long ago by Dezmazières. The perithecia occur on the living leaves. They are not preceded by conidia and are much smaller than those of *D. macrospora*, but otherwise are very similar. Therefore it may be supposed that in the phylogenetic system these two fungi are related. The lack of conidia cannot be a sufficient reason for separating them in the system.

The investigation of a number of species from the genera *Gloeosporium, Marssonina, Asteroma, Leptothyrium,* and *Entomosporium,* generally placed in the Melanconiaceae, gave results which were unexpected and surprising. All these fungi have conidial layers which originate in the epidermal cells or in the outer wall of these beneath the cuticle. A peridium is absent. What seems to be a

peridial covering over the conidial layer of *Leptothyrium* is only a secretion of black substance.

As to the ascospore fruits, three groups may be distinguished. The first group is connected with pyrenomycetous fungi; with perithecia of the genus *Gnomonia* and closely allied fungi. The second group is related to discomycetes, with the apothecia in *Pseudopeziza* and *Fabraea*. In the third group there are, again, perithecia belonging to the genus *Glomerella*.

These three groups of *Gloeosporium*-like fungi cannot be distinguished even now by mere microscopical examination.

In the first group, *Gnomonia platani* is very remarkable because it is polymorphic in its fruit bodies. The *Gloeosporium*-layers occur in summer on the leaves of *Platanus*, causing brown spots which follow the veins. They have been called *Gloeosporium nervisequum*. On dead leaves lying on the ground a second conidial fruit is produced; it is surrounded by a sort of wall and has been described as *Sporonema platani*, and also as *Fusicoccum veronense*. When the mycelium has entered the bark of young branches and killed them, a third kind of conidial fruit, *Discula platani* or *Myxosporium valsoideum* is formed beneath the lenticels. All these three kinds of fruit bodies, although so different that they have been classed in quite different groups of the Saccardo system, contain the same oblong one-celled conidia. The perithecia, *Gnomonia platani*, are found in spring on the fallen leaves. The ascospores are two-celled, the lower cell being very small. Proof of the connection has been given by infection experiments and by pure cultures on agar, the spores of all the fruit bodies producing the same characteristic mycelium. *Gnomonia quercina* and *G. tiliae* are two fungi of very similar behavior and morphologically nearly identical.

Another fungus of the first group, *Marssonina juglandis* has two-celled conidia, and the ascigerous stage, *Gnomonia leptostyla*, has spores consisting of two cells of equal size. Here also a second kind of conidium is produced; small one-celled rods which are not able to germinate. They occur in similar acervuli, or sometimes in the *Marssonina*-acervuli, mixed with the normal two-celled conidia. Infection with ascospores is easily accomplished on young leaves of walnut. With this fungus I succeeded in getting perithecia on agar.

Asteroma padi, a third type of this group, is characterized by the mycelium which will be discussed later. The conidial layer resembles *Gloeosporium*. After overwintering a *Gnomonia*-like fungus was found, containing two-celled but thread-like ascospores. It easily reproduces the *Asteroma* stage on inoculated leaves. The appearance of these three types in pure culture is, to be sure, different, but there are some similarities which cannot be overlooked and which point to the relationship of the three genera.

In the fourth type of this group, *Leptothyrium alereum*, I did not succeed in getting cultures on agar. The cause, perhaps, is that it is more closely adapted to parasitic life than the others. The spots, which it produces on the leaves, remain alive for a long time. On the overwintered leaves, perithecia appear, known as

Gnomoniella tubiformis and characterized by one-celled ascospores. Inoculation with these spores produces spots on which *Leptothyrium*-acervuli appear.

Let us now consider some examples of the second group of *Gloeosporium*-like fungi. *Gloeosporium ribes* is a true *Gloeosporium* with crescent-shaped conidia, producing a spot disease on leaves of currants. When overwintered leaves were kept moist, the ascospore stage was formed. It is a very small discomycete, a *Pseudopeziza*. The one-celled spores easily infect the host plant and on agar reproduce the crescent-shaped conidia.

The other relationships in this group of *Gloeosporium*-like fungi are quite similar, but there is no certain rule as to the number of cells in conidia and ascospores. *G. salicis* has one-celled conidia, and the ascospore-fruit, called *Pseudopeziza salicis*, has also one-celled spores. In *Marssonina fragariae*, the fungus of a disease of strawberries, both spore forms are two-celled, and the apothecia therefore have to be called *Fabraea*. But in a third case, a fungus on poplar, the conidial stage is a *Marssonia*, with two-celled conidia, and the ascospore stage is a *Pseudopeziza*, with one-celled spores. This is another example which shows that not too much stress should be laid on the number of cells in the spore.

We find the same connection of a discomycete with *Gloeosporium*-like conidial layers in *Entomosporium maculatum*, a fungus living on leaves of pear and quince. The apothecia have two-celled spores and may be classed as *Fabraea*. But the conidia are very different from those of *Gloeosporium*. They are four-celled, the cells forming a cross, and three of them each bearing a thread-like appendage. Therefore the ascospore fruit may be considered as a particular genus which I called *Entomopeziza*.

A peculiarity of several of these fungi is the production in winter on the fallen leaves of a conidial layer surrounded by a sort of peridium. They contain the same sort of conidia as do the ordinary layers, and recall in a way the *Sporonema* fruits of *Gnomonia plantani* mentioned before. In *Fabraea fragariae*, apothecia were found which contained both the characteristic two-called conidia of *Marssonina* and asci with the two-celled spores of *Fabraea*, and thus presented direct confirmation of the connection proved before by cultures. In agar-culture all these fungi grow well, producing conidia. But the colonies remain very small, in contrast with the fungi of the *Gnomonia* group which finally spread throughout the agar.

Little is know concerning the third group of the *Gloeosporium*-like fungi. The connection of *Gloeosporium fructigenum* and similar fungi with *Glomerella* has been proved by American authors. The conidia on germination produce dark colored appressoria, and this seems to me to be the principal difference between this group and the two others. I noted this peculiarity in several other species of *Gloeosporium* or *Colletotrichum*, in *Gloeosporium lindemuthianum*, *G. lagenarium* and *G. darlingtoniae*. The appressoria appeared appressed to the cover glass of the moist chambers at a distance from the conidia lying on the surface of the agar. It is possible that many of these fungi may be able to produce *Glomerella*-like perithecia, but I did not succeed in obtaining them in the species

cultivated by myself. The irregularities mentioned in my preceding communications show that it is not possible to solve mycological questions of this kind by analogy.

In addition to the fungi mentioned I have investigated a number of others, especially in the family Gnomoniaceae. As a general rule I may state that the behavior of apparently similar fungi is often very different, so that here also, each fungus requires its own investigation.

It has been shown in the preceding that several *Gnomonia*-like fungi are parasites and connected with conidial layers *(Gloeosporium)* on the living leaves. Another group of Gnomonias is saprophytic. I investigated *Gnomonia setacea, G. Vleugelii, G. carpinea, G. melanostyla, G. Stahlii, Hypospila pustula,* and others. Inoculation of the living leaves during the summer was unsuccessful but when the inoculated leaves had fallen and overwintered in the open air, ripe perithecia were found to be present in the spring. It must be concluded, that the spores or their germ tubes remain in a resting condition during summer, and that the mycelium does not begin to develop before the leaves die. Perhaps this is a behavior common to many fungi which appear in spring on the dead leaves lying on the ground. Another example of the same behavior, but in another group of fungi, *Mycosphaerella punctiformis* has already been mentioned. It is very remarkable that in agar-culture, while most of these Gnomonias freely produced perithecia, conidia were absent in almost all cases. *Gnomonia rosae* occupies an intermediate position between these saprophytic fungi and the true parasites. Inoculation of the leaves of roses gave no result for a long time, but two months after inoculation parts of the leaves turned brown; the leaves fell and when they were kept moist, perithecia began to develop in them.

I will return once more to the parasitic Gnomonias to mention *Gnomonia alniella* a very strange and interesting fungus. The spores, similar to those of *Gnomonia platani,* easily infect living leaves of *Alnus incana,* but on agar they refuse to germinate. Following inoculation brown and white spots appear on the leaves. Part of the mycelium enters the mesophyll. Another part spreads on the surface, in the outer walls of the epidermal cells in a characteristic dendritical manner, being only covered by the cuticle. Conidia are absent.

There are some other fungi which present nearly the same behavior of the mycelium, but otherwise are very different. *Asteroma padi,* the conidial stage of *Gnomonia padicola,* mentioned before, is one of them. It grows well in agar culture. *Actinonema rosae* is another one. According to Wolf it is the conidial stage of a quite different ascomycete, perhaps a discomycete or a *Microthyrium*-like fungus. It did not germinate on agar in Wolf's cultures nor my own. In a fourth case, *Stigmatea robertiani,* on leaves of *Geranium robertianum,* the mycelium does not enter into the mesophyll, but spreads only in the outer cell wall, below the cuticle, and the perithecia originate in the same manner. Conidia are absent. It is a very remarkable case of adapted parasitism. On agar, only very small cultures were obtained of less than ½ mm. in diameter.

Adaptation of parasites to a limited number of host plants or what is called

specialization is a very well known subject much investigated in the Uredineae. It has also been mentioned in Ascomycetes, but here perhaps it is not quite so frequent. *Pseudopeziza* or *Gloeosporium ribis* embraces several races, one adapted to red currants only, a second to black currants, a third to gooseberries, a fourth perhaps to *Ribis alpinum*. The race on gooseberries seems to have lost the power of producing apothecia; infection in spring seems to result only from the conidial layers formed during winter. *Pseudopeziza populi* or *Marssonina populi* is another example. The fungus on *Populus alba* infects only this tree, and the fungi on other poplars which have not yet been studied by infection experiments, present little difference in size and shape of the conidia.

I have confined my communications to my own research. I cannot enter here into a discussion of those fungi which I could not investigate myself. I began many years ago a compilation of all that has been stated or supposed about the connections of ascospore and conidial stages. Now I will try to sum up some of the general results of cultural work under the following heads: 1. In characterizing the genera of Ascomycetes the conidial stages must be noted. 2. As a rule, the conidial stages of nearly related Ascomycetes are similar to one another, but there are exceptions. 3. There may be differences between fungi which look alike which cannot be recognized by the common morphological methods. They can sometimes only be determined by studying the other related fruit form or by the behavior in culture. This proves as true for conidial fruits in their relation to ascigerous fruits as for the ascigerous fruits in relation to conidia. 4. Absence of a spore form does not exclude the possibility of relationship to a fungus which possesses this spore form. 5. The number of cells in a spore or a conidium is of little importance in a study of relationships. 6. In many cases Ascomycetes produce only one sort of conidia. 7. In other cases several sorts of conidial fruit bodies are present, all containing the same conidia. 8. In a third group of cases, microconidia are produced beside the macroconidia, in the same or in special fruit bodies. Generally they are not able to germinate. Their significance is unknown. 9. The classification of Ascomycetes and still more that of the imperfect fungi requires improvement. The common morphological methods are not sufficient. Cultures are indispensable in obtaining an accurate knowledge of the behavior and the relationships of fungi.

In concluding, allow me to say a few words concerning the family of Exoasci or Taphrinaceae. I published some time ago a short paper on *Taphrina Tosquinettii*. I succeeded in getting pure cultures on agar. All the eight spores of an ascus are ejected at once and may be found then lying together on the agar. They begin to produce conidia by yeast-like sprouting. No mycelium is formed. When conidia obtained in this manner are distributed in water and put on the buds of the host plant in autumn or early spring, abundant infections may be obtained. I induced one of my students, Miss U. Wieben, to continue these investigations. Pure cultures of several other species were obtained in the same manner, all consisting of nothing but conidia. Inoculations were successful on *Alnus glutinosa* by *Taphrina Tosquinetii*, on *Alnus incana* by *Taphrina epiphylla*, and on peach by

Taphrina deformans.   Over-wintering takes place by means of mycelium which has entered the buds.   In perennial species it penetrates to the growing point, in annual species like *Taphrina Sadebecki* or *T. aurea* it restricts itself to the outer-most leaves inside the brown scales, and reinfection of the buds must take place every autumn.   Therefore, it is possible that the fungus is abundant on a tree in one year and scarce or missing in the next year.

In some cases short mycelial threads were seen to grow out from the colonies of conidia in the agar cultures.   It was shown by investigation that they were the result of a conjugation and the beginning of the binucleate stage of the mycelial cells.   The spores ejected from any one ascus, are uninucleated.   Four are male and four are female.   The conidial descendants inherit the same sex.   Conjugation only takes place when conidia of different sex are lying near one another; it may be augmented by mixing the different descendants.   Two conidia unite by a bridge. The nucleus of one of them passes over into the other.   A germ tube is produced from this cell and both nuclei enter it.   The germ tube increases in length but the protoplasmic content does not increase, nor do the nuclei or the cell divide. The cells of the mycelium in the host plant always being binucleate, it must be concluded that the fungus does not enter the host tissue without conjugation of conidia.   It must be supposed that after infection conjugate division of nuclei and cell division begin to take place.

THE MORPHOLOGY, BIOLOGY, AND PHYLOGENY OF THE PUCCINIASTREAE[1]

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P. and H. Sydow in their "Monographia Uredinearum" recognize four families of rusts—Pucciniaceae, Melampsoraceae, the doubtful Zaghouniaceae (of two species only), and the Coleosporiaceae. The Melampsoraceae are further divided into four sub-families—Melampsoreae, Pucciniastreae, Chrysomyxeae, and Cronartieae. We are concerned here with the Pucciniastreae as defined in the Monographia.

Phylogenetically, the Coleosporiaceae are regarded by many as the most primitive of the rusts, with the sub-family Pucciniastreae as the next in order; but others give first place to the latter. There is general agreement, however, that the Pucciniastreae are at least primitive rusts. Because of this the group is an especially interesting one to study. For several years investigations have been in progress by the author, and at various times during that period by his student associates Messrs. H. P. Bell, W. R. Watson, E. H. Moss, G. D. Darker, E. H. Bensley, and Miss L. M. Hunter. This paper is designed to present a summary up to date.

The Pucciniastreae comprise not quite seventy-five known species, and these are distributed among eight genera—*Melampsoridium* (3), *Melampsorella* (2), *Pucciniastrum* (19), *Thecopsora* (8 or 9), *Calyptospora* (1), *Hyalopsora* (10), *Milesina* (18), and *Uredinopsis* (11). Life cycles have been determined for less than one-third of the number, and all of these prove to be heteroecious with the aecial stage on *Larix, Picea, Tsuga,* and predominantly on *Abies.* Table 1 gives the names of the species the complete life cycles of which are known, the names of their hosts, and of the investigators who have demonstrated their connections.

MATERIAL

The material studied in our work consisted of—(a). Dried specimens only of *Melampsoridium betulinum, Thecopsora Vacciniorum* (O, I stages), *Milesina Blechni* (O, I), *Uredinopsis Pteridis* (including part of the type *Peridermium pseudobalsameum* on *Abies grandis*), and *Peridermium rugosum* Jackson (O, I). (b.). Fresh, and fixed, as well as dried specimens of *Thecopsora Vacciniorum* (II, III), *Pucciniastrum Abieti-Chamaenerii, P. Epilobii, P. americanum* (II, III), *P. arcticum* (II, III), *P. Potentillae* (II), *P. Pyrolae* (II), *Melampsorella Caryophyllacearum, Calyptospora Goeppertiana, Hyalopsora Aspidiotus, H. Polypodii* (II, III), *Milesina marginalis, M. Kriegeriana, M. polypodophila, Uredinopsis americana, U. Struthiopteridis, U. Phegopteridis, U. Atkinsonii,* and *U. Osmundae.*

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TABLE 1

Rust	0, I Host	II, III Host	Investigator
Melampsoridium betulinum (Tul.) Kleb.	Larix	Betula	Plowright (1891), Klebahn (1898–9, 1902).
Thecopsora areolata (Fries) Magn.	Picea	Prunus	Tubeuf (1900), Fischer (1906), Klebahn (1907).
" *sparsa* (Winter) Fischer	Picea	Arctostaphylos	Fischer (1917).
" *Vacciniorum* (DC) Karst.	Tsuga	Vaccinium, Gaylussacia	Clinton (1909–10) Fraser (1913–14).
" *minima* (Arth.) Syd.	Tsuga	Rhodora	Fraser (1912).
" *Hydrangeae* (B. & C.) Magn.	Tsuga	Hydrangea	Adams (1920).
Pucciniastrum Abieti-Chamaenerii Kleb.	Abies	Epilobium (Chamaenerion)	Klebahn (1898·1900, 1901, 1905), Fischer (1900), Tubeuf (1902), Bubak (1906), Fraser (1912), Weir and Hubert (1916), Faull and Darker (1926)*
" *Epilobii* (Pers.) Otth.	Abies	Epilobium (Lysimachion)	Faull and Moss (1925), Faull and Darker (1926).
" *Circaeae* (Thüm.) Speg.	Abies	Circaea	Fischer (1917).
Melampsorella Caryophyllacearum (Link) Schroet.	Abies	Stellaria, Cerastium	Fischer (1901, 1903), Klebahn (1902), Tubeuf (1902), Bubak (1914), Stone (1920), Faull and Watson (1924).
" *Symphyti* Bubak	Abies	Symphytum	Bubak (1904).
Calyptospora Goeppertiana Kühn	Abies	Vaccinium	Hartig (1880), Kühn (1885), Bubak (1904, 1906), Klebahn (1904), Arthur (1909), Fraser (1912, 1914), Bell (1924), Faull and Watson (1924), Faull and Moss (1925).
Hyalopsora Aspidiotus (Peck) Magn.	Abies	Phegopteris Dryopteris	Mayor (1923), Bell (1924), Faull and Darker (1924–26).
Milesina Blechni Syd.	Abies	Blechnum Spicant	Klebahn (1916).
" *marginalis* Faull and Watson	Abies	Aspidium marginale	Faull and Watson (1924).
" *Kriegeriana* Magn.	Abies	" spinulosum	Faull and Watson (1924).
" *polypodophila* (Bell) Faull	Abies	Polypodium vulgare	Faull and Watson (1924).
Uredinopsis americana Syd.	Ab˙es	Onoclea sensibilis	Fraser (1912–14), Faull and Bensley (1926).
" *Struthiopteridis* Störmer	Abies	Onoclea Struthiopteris	Fraser (1913), Faull and Bensley (1926).
" *Phegopteridis* Arthur	Abies	Phegopteris Dryopteris	Fraser (1913), Faull and Moss (1925), Faull and Bensley (1926).
" *Atkinsonii* Magn.	Abies	Asplenium Filix-femina	Faull and Watson (1924), Faull and Moss (1925), Faull and Bensley (1926).
" *Osmundae* Magn.	Abies	Osmunda	Fraser (1913), Faull and Watson (1924), Faull and Moss (1925), Faull and Bensley (1926).
" *Pteridis* D.& H.	Abies	Pteridium aquilinum pubescens	Weir and Hubert (1917).

* The dates of publication, except those of the author and his associates, which are dates of experiments.

NEW SPECIES AND STAGES

In the course of our work the following new species or hitherto unrecorded stages have been obtained both in the field and in cultures:

1. Stages O, I of *Pucciniastrum Epilobii* (Pers.) Otth. These were on *Abies balsamea.*
2. Stages O, I of *Hyalopsora Aspidiotus* (Peck) Magn. on *Abies balsamea.* Spermogonia were first seen in the summer of 1919, and peridermia in the spring of 1922. In cultures, spermogonia first formed in the spring of 1925 and an abundance of peridermia on the same needles in the spring of 1926. Klebahn obtained the spermogonia in cultures on *Abies pectinata* in 1916 but did not see the aecial stage. Mayor found both spermogonia

and peridermia on *Abies pectinata* in 1919, and spermogonia in cultures on the same host in 1922, but the affected needles dropped off before peridermia were formed.

3. Stages O, I of *Milesina Kriegeriana* Magn. These were on *Abies balsamea*.
4. Stages II, III, of *M. Kriegeriana* on *Aspidium spinulosum* in America.
5. Stages O, I of *Milesina marginalis* Faull & Watson. These were on *Abies balsamea*. Stage III on *Aspidium marginale*.
6. Stages O, I, II, III of *Milesina polypodophila* (Bell) Faull. These were found on *Abies balsamea* and *Polypodium vulgare*.
7. Stages O, I, II, III of *Uredinopsis Aekinsonii* Magn. as found on *Abies balsamea* and Asplenium *Filix-femina*.

It is of interest to record that of the 17 species listed in Table I as parasitic on Abies, 13 have been found on *Abies balsamea,* that is all except *Melampsorella Symphyti, Pucciniastrum Circaeae,* and *Milesina Blechni,* which are European, and *Uredinopsis Pteridis*. All thirteen occur on *Abies balsamenea* in such a restricted area sa Bear sland, Lake Timagami, Ontario, all within a radius of half a mile, and all have been located by the author in vriaous parts of Ontario and Quebec.

MORPHOLOGY

(a). *Mycelium.* The mycelium is typical in that it is endophytic and intercellular. Interest centers, however, in the haustoria, and attention was given to them for the aecial and telial hosts by Hunter and Moss respectively. They were found in all species recorded above under "Material (b)," that is, in all the species of which we had properly fixed material. In many species they were noted for the first time, and they have been demonstrated for *Uredinopsis,* in which genus it has been claimed that they are absent. It is worth recording that they are more or less characteristic for each genus. Moss finds that sheaths covering the haustoria are frequent in the telial hosts, and Hunter that they are rare on the aecial. The sheaths form from the base upwards on mature haustoria, and are laid down by the protoplasm of the host cells and not as an invagination of the walls as DeBary and others have thought. It seems likely that the protoplasmic membranes are not broken by the invading branches, but, pushed inwards, grow or stretch to keep pace with the extending haustoria.

(b). *Spermogonia.* Hitherto, not much attention has been paid to the spermogonia of the Pucciniastreae, but observations in the field and careful comparative histological studies, the latter mainly by Miss Hunter, have secured some striking results. In general there is a characteristic type of each genus, and these types are similar for genera that on other grounds might be considered more closely related. In some cases the forms within a type are distinctive for individual species.

Largest and most conspicuous of all are the spermogonia of *Hylalopsora Aspidiotus* (the O stage of *Peridermium pycnoconspicuum* Bell). They are large flat, brownish orange, subepidermal disks, with a marked development of mycelium at their bases. They make their appearance on second year needles, just one year following infection, and one year in advance of the peridermia. The period of spermatial discharge is exceptionally long, lasting approximately one month according to records made by Darker for 1925 and 1926.

The spermogonium of *Uredinopsis* is of the hemispherical type, with its rounded base well depressed in the host tissues. Though of moderate size, it can be observed only with careful attention through a hand lens because it is colorless and submerged. It begins its development under the cuticle, but the underlying epidermal cells are destroyed, or separated, crushed and pushed downwards by the enlarging organ. The spermogonium of *U. Pteridis* is very much larger than in any of the other species of *Uredinopsis*. It occurs on second year needles along with the peridermia, but whether formed in the same season or in the preceding year no one seems to have observed. The spermogonia of the other species of the genus perhaps cannot be distinguished from one another, but the examination of this point is still incomplete. They all occur on the needles of the current season only, just as do their corresponding peridermia. Their rounded bases are distinguished by large, cylindrical, elongated, radially disposed, closely compacted cells, from which the more slender spermatophores grow centripetally towards the oral aperature.

The spermogonium of *Milesina* is also of the hemispherical type, colorless, submerged, with a rounded base. That of *M. Kriegeriana* is about the same size as in *Uredinopsis americana*, etc., but is more rounded, the basal cells are much shorter and the spermatophores usually not so compacted. The spermogonium of *M. marginalis* is very much larger, and this feature in itself would serve to distinguish this species from the last. In both cases the origin is subcuticular with further development as in *Uredinopsis*. The spermogonium of *M. polypodophila* (the O stage of *Peridermium pycnograndé* Bell) is remarkable in many ways. It is relatively huge, deeply thrust into the mesophyll, subepidermal, but not conspicuous because of its lack of color. It never appears on the needles of the current season, as is true of the others, but for the first time following primary infection on third year needles, after which there are crops in succeeding years on the needles of the contiguous areas in both directions. There is an especially abundant, long-continued spermatial discharge; at times during this period the affected needles are wetted by the fluid discharged along with the spermatia just as though they had been immersed in an adhering liquid.

In contrast to *Hyalopsora, Uredinopsis,* and *Milesina,* the spermogonia of *Melampsoridium, Thecopsora, Pucciniastrum, Melampsorella,* and *Calyptospora* are very small, their bases are flattened, and they rest on the epidermal cells under the cuticle without destroying or depressing them. Detailed studies were made from paraffin sections, but in the case of *Melampsoridium* and *Thecopsora* dried material only was available, so that observations on them were necessarily incomplete. As for the remaining three, the spermogonia of *Melampsorella Caryophyllacearum* are distinctly the largest. They are conspicuous, bright orange, cushion-shaped bodies, rounded well up above the surface of the needle. The stretched cuticle over them ruptures suddenly and extensively, and spermatial discharge is of brief duration. The spermogonia of *Pucciniastrum Abieti-Chamaenerii* and *P. Epilobii* are tiny, subconical, and very slightly elevated. Seen with a good hand lens they look like yellow points in the epidermis. Their spermatia are dis-

charged through a small apical opening. Whether or not there are spermatia in *Calyptospora Goeppertiana* has long been questioned. But paraffin sections of properly fixed material show that they do occur, and often in rather large numbers. They are apparently colorless and can be scarcely detected with a hand lens. Sections show that they are aborted to the extent that spermatia are not formed, and as a rule the overlying cuticle is unruptured. If spermatia do develop and mature it must be rarely and sparsely.

(c). *Aecia.* The aecial stage of the Pucciniastreae is characterized throughout by a *peridermium.* The peridium of this organ is delicate and colorless; the contained spores of *Milesina* and *Uredinopsis* are likewise colorless, but the spores of all the others are yellow. Two contributions of special interest have resulted from our studies, first, new or confirmatory information relative to the length of the period from inoculation to the first appearance of the peridermia, and second, the status of *Peridermium balsameum.*

In connection with the first point two forms stand out as especially remarkable, namely, *Hyalopsora Aspidiotus,* and *Milesina polyodophila.* The peridermia of *H. Aspidiotus* occur typically on third year needles, never earlier, that is, two full years after inoculation, for infection takes place only in newly unfolded leaves. Occasionally the appearance of the peridermia may be deferred to the fourth or in very exceptional instances to the fifth year. It also happens that the same needle may bear peridermia in two successive seasons. The same phenomena are true of *M. polypodophila.* But in the latter the mycelium stimulates the host to form loose brooms, and it spreads downward and upward in the branches for many years, producing crops of peridermia on the old needles of the newly invaded zones. Its peridermia have been found on needles of the third to the ninth year, that is on needles two to eight years old. Fischer worked out the life history of the broom forming *Melampsorella Caryophyllacearum* and discovered that the first spermogonia and peridermia appear in the first year after inoculation, but, of course only on the needles of the current season, because the brooms are completely defoliated each year.

In all of the other rusts studied the peridermia are found on the needles of the current season only and there is a brief period of development. Our summarized data (from eperiments made by Faull, Darker, Watson, Moss, and Bensley), for the time period betwen inoculation and the emergence of the peridermia are as follows:

Pucciniastrum Abieti-Chamaenerii	15-20 days
Pucciniastrum Epilobii	23-32 days
Calyptospora Goeppertiana	17-22 days
Milesina Kriegeriana	33-36 days
Milesina marginalis	41-51 days
Uredinopsis americana	21-25 days
Uredinopsis Struthiopteridis	20-24 days
Uredinopsis Phegopteridis	23-25 days
Uredinopsis Osmundae	22-28 days
Uredinopsis Atkinsonii	23-27 days

Turning to the second point we find that *Peridermium balsameum* was a name given by Peck to a white-spored *Peridermium* on *Abies balsamea*. On the assumption that there was only one white-spored species on this host, the name has long passed current for all its white-spored peridermia. Fraser was the first to demonstrate that five species of Uredinopsis alone pass to *Abies balsamea* and that the aecial stage of each answered to *Peridermium balsameum*. Our own work has confirmed Fraser's and we have extended the study to *Milesina*, uncovering three additional species all of which likewise have white-spored Peridermia on *Abies balsamea* They, too, would and probably have passed for *Peridermium balsameum*. The case of *P. pseudocolumnare* Kühn on *Abies pectinata* in Europe is identical, so that neither of these names appears to be of any value or standing—at all events not until someone determines from the types to exactly what particular rusts they belong.

(d) *Uredinia.* Field and laboratory observations have been made on the uredinia of the Pucciniastreae by Bell, Darker, Moss, and Faull.

Dr. Moss has just completed a histological survey of the uredinia of the entire subfamily, especially from the developmental point of view. Species of all of the genera were included, and satisfactory material was available for all except *Melampsoridium*. Two main problems were investigated by him, namely, the origin of the peridium, and the mode of spore production.

So far as is known a peridium is a constant, uniformly present, uredinial structure throughout the Pucciniastreae. As it is a very delicate colorless membrane its presence cannot always be very well ascertained from dried specimens, but it can always be found in properly fixed, sectioned uredinia of all ages. The peridium consists of the laterally adhering apical cells of the 3-celled vertical columns which constitute the initial stage of the young subepidermal uredinium. The middle cells of the columns are sister cells of these, and they soon disintegrate leaving an enclosed uredinial chamber, the floor of which is made up of the large basal spore-producing cells. As a result of expanding growth the middle cells of the peridial roof separate or rupture leaving a centrally placed ostiole. The amphiostiolar cells may become quite highly specialized, as in *Pucciniastrum americanum*. In most genera the uredinium is located directly under a stoma of the over-lying epidermis.

As already stated the basal cells of the initial columns are sporogenous. The uredospores are produced singly from them by a budding-off process, and they are produced singly and not in chains—in *Melampsorella, Pucciniastrum*, and *Uredinopsis* as well as the rest. Buds may form successively from the same mother cells, but not catenulately. From each bud a spore and short stalk cell are cut off. It is, of course, possible that occasionally spores may arise catenulately, and at times it is difficult to decide positively whether or not such may not be the case, but no undoubted instances were observed by Moss.

In passing, reference should be made to the two known types of uredospores which have been reported for a few of the fern rusts. We have found them in *Hyalopsora Aspidiotus, H. Polypodii, Uredinopsis Atkinsonii, U. americana,* and

U. Struthiopteridis, but in none of the others.   There are thin-walled spores in these species that appear in the earlier uredinia; subsequently thick-walled spores of different size and markings develop in increasing numbers, until in the later uredinia these only may be found.   The thick-walled spores winter over and so the rust may be perpetuated without the mediation of the aecial host.   Of course, this same feature is accomplished in some of the Pucciniastreae by a mycelium that is perennial in the telial host, as for example, in *Hyalopsora Aspidiotus,* and in *Melampsorella Caryophyllacearum.*   Moss thinks that the type of spore is related to the age of the host leaf and not to the season; the first spores on new leaves, no matter when the leaves appear, are thin-walled.   The uredospores of Pucciniastreae are all provided with one or more germ pores.

(e). *Telia.*   The teliospores of the Pucciniastreae are subepidermal or intra-epidermal, and are arranged in single-layered, diffuse crusts.   They are subepidermal in *Melampsoropsis, Pucciniastrum* and *Uredinopsis,* and intraepidermal in the remaining five genera.   The crusts are of no definite form or extent, and the number of comprised spores varies within the widest possible limits; hence the term sorus or telium can be used only in a very indefinite sense.   Thus in *Calyptospora Goeppertiana* the epidermis of an entire stem is involved, though the microscope shows that there are empty cells scattered throughout; in a *Milesina,* or in *Melampsorella Caryophyllacearum,* or in *Hyalopsora Aspidiotus* the lower epidermis of an entire leaf may be involved, or just irregular patches, and in both cases only a part of the cells are occupied by spores.   At the same time there are, commonly, isolated cells of the upper epidermis of the lesions with one or more spores.   In a *Uredinopsis* the spores are more or less numerous under the lower epidermis within the limits of isolated leaf eyelets, or of a variable number of contiguous leaf eyelets, and occasional single spores under the upper epidermis. In a *Pucciniastrum* the crusts are less poorly defined, but the number of spores is extremely variable.

Regarding *Uredinopsis* there is a general misconception.   Sydow and Dietel describe and figure the spores as solitary, scattered through the mesophyll and rarely under the epidermis; Gäumann in his new text, "Vergleichende Morphologie der Pilze," classes them with those of *Melampsorella* as being capable of immediate germination, and states that they are not resting spores, while Grove informs us that they are resting spores irregularly scattered throughout the spongy mesophyll, so deeply seated that decay of the host tissues must take place before germination. As a fact, the spores are typically placed just under the epidermis. They overwinter and germinate promptly in the spring, the basidia boring through the overlying undecayed epidermis.

There are exceptional irregularities in the distribution of the teliospores of the Pucciniastreae which may or may not be of significance.   Thus in *Uredinopsis* and *Pucciniastrum* they may occasionally be found at various points in the mesophyll; and in *Milesina,* where they are typically intra-epidermal, a few may not infrequently be found located under the epidermis, or within the cells of the mesophyll, or in the intercellular spaces.   Another exception is to be found in the sporadic

doubling of the crust in very restricted areas, ordinarily within the limits of one or two spores.

The spores are mostly septate, and the septa are anticlinal. In *Melampsoridium* they are regularly unicellular and in *Melampsorella* commonly so. Unicellular spores are more or less frequent in all of the other genera, but generally they are divided into two or more cells. In all cases the cells are occupied by two nuclei at the outset, and these subsequently fuse. The most peculiar spores are those of *Hyalopsora* and *Milesina*, where they are often irregular, multiseptate disks, conforming more or less in shape to the irregular outlines of the containing epidermal cells.

There is a germ pore for each cell of a teleutospore, except apparently for *Uredinopsis*, where as yet pores have not been demonstrated.

The teliospores of *Melampsoridium, Thecopsora, Pucciniastrum,* and *Uredinopsis* develop on the leaves, and of *Calyptospora* on the stems of the current season, and overwinter. Those of *Melampsorella Caryophyllacearum, Hyalopsora Aspidiotus,* and *H. Polypodii* develop on the new leaves first thing in the spring, and germinate at once. The former we have found on *Stellaria graminea* in the Timagami Forest Reserve. The three species of *Milesina* present an interesting departure, in that they develop in the spring, not on new fronds, but on overwintered leaves. They mature rapidly and germinate without a resting period. In *M. Kriegeriana* they are found on large dark-colored spots on the leaves; in *M. marginalis* they may cover the entire under surface of a frond, their presence being indicated by a rich brown-colored epidermis; the same thing is also true of *M. polypodophila,* but the infected areas are much more limited in extent.

(f). *Basidiospores.* The basidia and their spores are of the ordinary type. The former bore through the overlying epidermal membranes, and are evident as a delicate whitish bloom. The spores mature at about the time the needles of their coniferous hosts have expanded.

BIOLOGY

We have carried on a good deal of culture work on the Pucciniastreae during the last three years, 1924-26, and in this Messrs. Darker, Watson, Moss, and Bensley have co-operated. Where telial material has had to be overwintered the practice has been to collect it in the fall, and place it in net packets out of doors. If prematurely warm spring weather favors germination before the coniferous hosts have come into leaf, germination can be readily and safely delayed by transferring the material to an icebox during such periods.

A list of our culture experiments is presented, with results in Table 2. The experiments believed to be new are marked with an asterisk. The initials W, M, D, B, are of the co-operating experimenters. All experiments were carefully and successfully controlled. Positive results are marked P, negative results N.

PHYLOGENY

In considering the possible phylogeny of the Pucciniastreae we have to deal with a fairly complicated set of facts. The principal ones appear to be as fol-

TABLE 2

Rust	From	To	Result
Melampsorella Caryophyllacearum	Abies balsamea	Stellaria graminea	P.(W)
" "	" "	" media	P.(W)
" "	" "	Cerastium vulgatum	P.(W)
Pucciniastrum Epilobii	Epilobium adenocaulon	Abies balsamea	P.(M) (D)
" "	Abies balsamea	E. adenocaulon	P.(D)
" "	" "	E. angustifolium	N.(D)
P. Abieti-Chamaenerii	Epilobium angustifolium	Abies balsamea	P.(D)
" " "	Abies balsamea	E.angustifolium	P.(D)
" " "	" "	E.adenocaulon	N.(D)
Calyptospora Goeppertiana	Vaccinium pennsylvanicum	Abies balsamea	P.(W)
" "	" canadense	" "	P.(D)
Hyalopsora Aspidiotus	Phegopteris Dryopteris	" "	P.(D)
" "	Abies balsamea	Phegopteris Dryopteris	P.(B) (D)
" "	" "	Cystopteris fragilis	N.(D)
" "	" "	" bulbifera	N.(D)
" "	" "	Scolopendrium vulgare	N.(D)
" "	Phegopteris Dryopteris	P. Dryopteris	P.(D)
" "	" "	Cystopteris fragilis	N.(D)
" "	" "	" bulbifera	N.(D)
" "	" "	Scolopendrium vulgare	N.(D)
Milesina marginalis	Aspidium marginale	Abies balsamea	P.(W)
" "	Abies balsamea	Aspidium marginale	P.(W)
M. Kriegeriana	Aspidium spinulosum	Abies balsamea	P.(W)
" "	Abies balsamea	Aspidium spinulosum	P.(W)
M. polypodophila	Polypodium vulgare	Abies balsamea	P.(W)
" "	Abies balsamea	Polypodium vulgare	P.(W)
Uredinopsis americana	Onoclea sensibilis	Abies balsamea	P.(B)
" "	Abies balsamea	Onoclea sensibilis	P.(B)
" "	" "	Osmunda claytoniana	N.(B)
" "	" "	" regalis	N.(B)
" "	" "	" cinnamomea	N.(B)
" "	" "	Asplenium Filix-femina	N.(B)
" "	" "	Onoclea Struthiopteris	N.(B)
" "	" "	Phegopteris Dryopteris	N.(B)
U. Struthiopteridis	Onoclea Struthiopteris	Abies balsamea	P.(B)
" "	Abies balsamea	Onoclea Struthiopteris	P.(B)
" "	" "	" sensibilis	N.(B)
" "	" "	Osmunda claytoniana	N.(B)
" "	" "	" regalis	N.(B)
" "	" "	" cinnamomea	N.(B)
" "	" "	Asplenium Filix-femina	N.(B)
" "	" "	Phegopteris Dryopteris	N.(B)
U. Atkinsonii	Asplenium Filix-femina	Abies balsamea	P.(M)
" "	Abies balsamea	Asplenium Filix-femina	P.(M)
" "	" "	Osmunda claytoniana	N.(M)
" "	" "	" regalis	N.(B)
" "	" "	" cinnamomea	N.(B)
" "	" "	Onoclea sensibilis	N.(M)
" "	" "	" Struthiopteris	N.(B)
" "	" "	Phegopteris Dryopteris	N.(M)
Uredinopsis Osmundae	Osmunda claytoniana	Abies balsamea	P.(B)
" "	Abies balsamea	Osmunda claytoniana	P.(B)
" "	" "	" regalis	P.(B)
" "	" "	" cinnamomea	N.(B)
" "	" "	Onoclea sensibilis	N.(B)
" "	" "	" Struthiopteris	N.(B)
" "	" "	Asplenium Filix-femina	N.(B)
" "	" "	Phegopteris Dryopteris	N.(B)
U. Phegopteridis	Phegopteris Dryopteris	Abies balsamea	P.(B)
" "	Abies balsamea	Phegopteris Dryopteris	P.(B)
" "	" "	Osmunda claytoniana	N.(B)
" "	" "	" regalis	N.(B)
" "	" "	" cinnamomea	N.(B)
" "	" "	Onoclea sensibilis	N.(B)
" "	" "	" Struthiopteris	N.(B)
" "	" "	AspleniumFilix-femina	N.(B)
U. Osmundae	Osmunda claytoniana	Osmunda claytoniana	P.(B)
" "	" "	" regalis	P.(B)
" "	" "	" cinnamomea	N.(B)

(Aeciospores used where the transfer was from *Abies* to ferns were obtained from peridermia on *Abies* which had been inoculated with telia from *Osmunda claytoniana*).

lows. (1) The species of three genera, namely, *Uredinopsis*, *Milesina*, and *Hyalopsora*, are restricted to *Abies* and ferns, while the others are found on *Abies*, or *Larix*, or *Picea*, and Angiosperms. In the case of the last none are known on the most recent Angiosperms, such as the Orchidaceae or the Compositae. (2) The yellow rust pigment is entirely absent in two genera, *Uredinopsis* and *Milesina*, and present in all of the others. (3) The spermogonia are comparatively large and deep-seated in three genera, namely, *Uredinopsis*, *Milesina* and *Hyalopsora*, and small

Pucciniaceae

Melampsoreae

Calyptospora

Thecopsora

Melampsoridium

Pucciniastrum

Coleosporiaceae

Melampsorella

Chrysomyxeae

Cronartieae

Hyalopsora

Milesina

Uredinopsis

and superficial in the others, becoming measureably aborted in *Calyptospora*. (4) The peridermium is fairly constant throughout. (5) The uredinium is also quite constant, except for the fact that it is entirely absent in *Calyptospora*. But it is largest in *Uredinopsis*, and its peridium is simple in such genera as *Uredinopsis*, *Milesina*, *Hyalopsora*, and *Melampsorella*, and shows specialization in species of *Pucciniastrum*, *Thecopsora*, and *Melampsoridium*. (6) The telia are diffuse, but most strikingly so in *Uredinopsis*. They are also markedly diffuse in *Milesina*,

Hyalopsora, and *Melampsorella,* but tend to become more compact in *Pucciniastrum, Thecopsora,* and *Melampsoridium.* They are compact in *Calyptospora* through widely extended. (7) The teliospores are subepidermal in *Uredinopsis, Pucciniastrum* and *Melampsoridium,* but are located in the epidermis in the other genera. The sub-epidermal position in *Milesina* especially is sporadically not infrequent. (8) The teliospores are irregular in form and in cell-number in *Milesina* and *Hyalopsora.*

Regarding the evidence as a whole, *Uredinopsis* appears to be the most primitive genus, with *Milesina* as a close relative. The appended diagram shows the approximate relationships in the judgment of the author.

As to the Cronartieae and the Chrysomyxeae, they are apparently offshoots from near the base of the Pucciniastreae, and are marked especially by a specialization of the telial sorus. Of the two the Chrysomyxeae have advanced the further in that their uredospores develop catenulately and with intercalary cells. The Melampsoreae are evidently quite closely related to the Pucciniastreae, though it is possible that they are not monophyletic. Some of them as judged by their host relationships and spermogonia have originated from rather primitive Pucciniastreae. The vestigial occurrence of peridia is also of significance. The Coleosporiaceae are comparatively specialized. Their telia are compact, their hosts include the Compositae; in the sub-family Ochrosporeae there is what may be regarded as a vestigial uredinial peridium, and in this same subfamily the uredospores originate singly.

PRESENT EVOLUTIONARY TENDENCIES AND THE ORIGIN OF LIFE CYCLES IN RUSTS[1]

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PRELIMINARY ABSTRACT

One of the most outstanding features of the Uredinales is to be found in the presence of the various types of life cycle. When all the spore forms of a given species are known it is possible in general to assign it to one of the several types of life history commonly referred to as eu-, -opsis, brachy-, or micro- forms. The first three of these forms are macrocyclic and the last may be designated as microcyclic.

Cytological investigations have shown that there are two essential periods in the life cycle of rusts. The first of these is the fusion of two cells of the haploid generation to form the first cell of the diploid phase. The other essential point involves the union of the paired nuclei in the teliospore and the reduction divisions which follow in the development of the basidium (promycelium).

The normal or orthodox type of life history as exemplified by *Puccinia graminis* or *Phragmidium subcorticium* is too familiar to need review. It may be well to point out that in the brachy- forms the aecium bears urediniospores as the first spore form following the cell fusions. The sorus is an uredinoid aecium sometimes spoken of as a primary uredinium. In many of the micro- forms the primordium of the sorus is aecidioid and the fusion cells are formed in the usual position but the only spore form developed is the teliospore. In *Endophyllum* and *Kunkelia* the aeciospores function as teliospores.

From the above it is evident that among the various types of life cycle any of the major spore forms—aeciospores, urediniospores, or teliospores may follow immediately after the formation of the fusion cells. While not so obvious it is nevertheless true that in any given species the potentiality exists for the immediate production of any spore form which occurs in the life history, as soon as the fusion cells are formed. In accordance with this reasoning, teliospores may be produced in aecial sori or telia may be borne on the same mycelium as that which produces aecia or primary uredinia. Teliospores may appear in the primary uredinia of brachy- forms, etc. The development of spores in such anomalous situations offers no difficulty so far as the nuclear phenomena are concerned.

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, Aug. 20, 1926.

It is in general true that the great majority of the species of rusts are apparently fixed and stable as to life history. If one searches for them, however, species may be found which have a composite life cycle and may be referred to as mutable species. The following species exhibit this condition in more or less degree: *Puccinia Helianthi, P. Podophylli, P. orbicula, P. effusa, P. insperata, P. punctata Uromyces fuscatus, U. Suksdorfii,* etc.

All of the hypothetical situations mentioned in the second preceding paragraph may be found in some of the species mentioned above. In *P. Helianthi* and *P. punctata,* for example, it has been shown by culture experiments that the haploid mycelium may produce as the aecial structure either an aecidium or a primary uredinium, in either case accompanied by pycnia. *Puccinia orbicula* is apparently similar. One may find on a single leaf infected by this species, pycnia with aecidia, pycnia with primary uredinia or pycnia with primary uredinia in which teliospores predominate. In this species both primary uredinia and aecidia may develop from the same mycelium. Teliospores have been observed in the aecidial cups of a number of species. The peculiar composite situation in *Puccinia Podophylli* has been quite fully investigated.[2]

From a study of such forms it is apparent that there is an inherent tendency in certain species of the Pucciniaceae at least to a simplification in life history. The microcyclic forms as well as the -opsis and brachy- forms have been derived directly or indirectly from the eu- forms.

ORIGIN OF MICRO- FORMS

It would appear that the micro- forms have been derived in part directly from the eu- forms and in part indirectly through the -opsis or brachy- forms. Their method of origin from the eu- forms furnishes the clue to the manner of origin of the other types of life history.

The combined evidence offered by a consideration of the following topics has been carefully analyzed as a part of this study: (a) species exhibiting a composite life history; (b) correlations between micro- forms and heteroecious eu- forms, (for example, *Puccinia mesneriana* and *P. coronata*); (c) the presence of occasional vestigial (?) aeciospores and peridial cells in the sori of micro- forms; (d) the absence of pycnia (conservative organs) in the life history of the majority of species of micro- forms (recognized in only 16 out of 148 North American species of *Micropuccinia*); (e) the close resemblance of the primordium of the sorus of micro- forms to that of aecidia as shown by cytological studies, etc. As a result of this analysis the writer ventures the hypothesis that a large majority of the micro- forms (of *Puccinia* and *Uromyces*) have been derived directly from the haploid generation of heteroecious eu- forms. As a working hypothesis it may be further suggested that the change is presumably in many cases an immediate one. The haploid mycelium developing on the alternate host simply pro-

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[2] Whetzel, H. H., Jackson, H. S., and Mains, E. B. The composite life history of Puccinia Podophylli Schw. Journ. Agr. Res. **30**: 65-79. 1925.

duces a sorus of teliospores instead of an aecidium. These teliospores are essentially like the teliospores of the parent heteroecious eu- form in morphology and are capable of reinfecting the aecial host. This new micro- form gives rise to a new race which continues to perpetuate itself and to bear teliospores only and always occurs on the aecial host of the macrocyclic species from which it was derived. Such a form is in effect an off-shoot or "life cycle mutation" of the original eu- form.

In the formation of such a micro- form the parent species may not completely change to the new type of life history but may continue to exist and to carry out its orthodox life cycle as before. The two forms continue as parallel "species."

It appears probable that the influence which brings about this change occurs sporadically and perhaps intermittently throughout only a part of the range of the parent species, so that the resulting form does not necessarily have the same range, or a single time or place of origin.

Such a sporadic origin of micro- forms would perhaps account for the varying reports of cytological detail which different investigators have made in studying the same species in different localities. If the hypothesis is correct it would not be surprising to find races existing in some forms which show differences in the cytological details of their life history.

While the great majority of short-cycled forms may have arisen from heteroecious eu- forms in the manner suggested, a few have doubtless arisen in an entirely similar manner from autoecious species. Others may have arisen through -opsis or brachy- forms in a somewhat different manner.

It should be recognized that many microcyclic species are known which cannot be correlated with the parent macrocyclic form. Any effort to work out correlations is limited by the incomplete knowledge with reference to the full life cycle of many heteroecious rusts. In some cases the long cycle form has presumably disappeared and the microcyclic form derived from it now stands alone. In others it is conceivable that there may have been a progressive development in morphology since their origin and that, because of this fact, their relationship can no longer be traced.

ORIGIN OF ENDOPHYLLUM

The species of *Endyphyllum* may be derived in an entirely similar manner from the haplont of heteroecious eu- forms in *Puccinia* and *Uromyces*. All the species occurring in temperate regions can be more or less fully correlated with the eu- forms from which they are derived. *Endophyllum uninucleatum* would be interpreted as a uninucleate race of *E. Euphorbiae-sylvaticae* and it in turn as a life-cycle race of *Uromyces Pisi* or related species. In a similar way *Kunkelia* may be derived from *Gymnoconia*. Cytologically distinct races exist in this form also (Dodge).

In general, the microcyclic species of *Puccinia* and *Uromyces,* the species of *Endophyllum* and *Kunkelia,* and perhaps most of the short-cycled rusts in other groups which show close correlation with macrocyclic species may be interpreted as life-cycle races of the latter.

ORIGIN OF -OPSIS FORMS

The explanation of the origin of the -opsis forms is somewhat more difficult. In general, the evidence would indicate that -opsis forms have not arisen from eu- forms by the simple expedient of dropping the urediniospores. The process is more complicated. Some of them can be derived by direct origin from the gametophyte of heteroecious eu- forms as outlined for the microcyclic rusts. In such cases both the aecia and the telia are retained in the resulting species (*Puccinia consimilis*, *P. commutata*, *P. microica*, *P. gigantispora*, *P. opposita*). Only a few of the existing species of -opsis forms can be derived in this way, however. In some of the forms originating in the manner suggested there is evidence that the aecia may not be functional, but that they merely continue to be developed in association with the telia. (*P. microica* is an example. Such species are in effect microcyclic.)

The basidiospores developed from the teliospores formed on the aecial host are capable of reinfecting that host and thus perpetuating the new form. Where the tendency to the development of aecia in association with the telia was retained this would result in an -opsis form of the type of *P. commutata*. It is entirely possible also that the influence which resulted in the tendency to change and throw off this -opsis form might also affect the aeciospores so that they were able to infect the aecial host, in which case we would have the development of summer telia. This might account for the origin of many typical -opsis species.

Many -opsis forms can be derived from autoecious rusts in a somewhat similar manner. It has been noted in a number of existing species of autoecious macrocyclic species, *Puccinia insperata*, *Uromyces fuscatus*, *U. Suksdorfii*, etc., that collections of the aecia made early in the season often have associated with them telia which evidently are developed from the same mycelium. Often teliospores are to be found developing within the peridium of an aecium. Usually they are grouped around or among the aecia. When collections of these species are made later in the season, however, one finds scattered uredinia and telia. In a number of cases the early collections have been described as separate -opsis species (*Uromyces Betheli* and *U. Rickerianus*). It is to be noted that in such forms there is a tendency for only a few uredinia to be formed. It frequently happens that collections show only a few urediniospores in the telia. Such cases indicate that there is an inherent tendency toward some profound change in the species.

When a long cycled autoecious species shows this tendency to the production of telia with the aecia we often obtain conditions typical of -opsis species. This suggests that from such species we can obtain the clue to the origin of many -opsis forms. The change which results in the development of teliospores on the haploid mycelium may result in a species exactly comparable to those which have arisen from heteroecious rusts as explained above. In this case the aecia would be retained and would for a time continue to behave as normal aecia of the original species, the aeciospores from which would produce uredinia and telia. The teliospores associated with the aecia have, however, a slightly different history from those of the long-cycled form, and it is conceivable that from these a new race arises

which tends gradually to the elimination of the urediniospores. We would then have a typical -opsis form developing parallel with the original eu- form. If, however, the change took place in the species simultaneously throughout its range and the tendency to the immediate production of teliospores were strongly enough established, the original species would disappear and the -opsis form would replace the eu- form.

ORIGIN OF BRACHY- FORMS

The brachy- forms (those which possess pycnia, uredinia, and telia) may be quite simply derived from autoecious rusts. One has only to study rusts which show the peculiar variations of *P. orbicula* and some other species to obtain a complete picture of the probable origin of this type of rust.

The brachy- forms have been derived simply by development of urediniospores on the haploid mycelium as the first spore form following the cell fusions. The aecidium would thus be eliminated. Judging from the situation found in *P. Helianthi, P. orbicula,* and others, the process is a gradual one, both types of life cycles apparently continuing through many generations.

It should be noted that pycnia are presumably always retained in a true brachy- form. Where pycnia are absent then the life history is uncertain. It is also worthy of note that the brachy- forms are apparently of quite recent origin. There are no rusts of this type of life history except in the Pucciniaceae. Among the 66 North American species of the Arthurian genus *Bullaria*, there are no species on Monocotyledons. Only nineteen species occur on Polypetalae and all are on the more recent families. All of these are sub-tropical except 5 which occur on Umbelliferae. Thirty-seven of the 66 species occur on Compositae.

Some micro- forms can be derived through the brachy- forms by the development of teliospores as the first spore form following the cell fusions. In this way the aecidium as well as the primary and secondary uredinia would be eliminated. The origin of the great majority of the micro-forms derived from autoecious rusts can perhaps best be accounted for by this method.

Finally, it should be emphasized that the micro- forms, the *Endophyllum* and *Endophyllum*-like forms, many if not all of the -opsis forms, and all of the brachy- forms are to be derived from the eu- forms through a change which is first expressed in the spore form developed on haploid mycelium.

CYTOLOGICAL EVIDENCE BEARING ON THE SEXUALITY AND ORIGIN OF LIFE CYCLES IN THE UREDINEAE[1]

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Of the many contributions coming from the Dangeard Laboratory in Paris, none has been so fertile in stimulating cytological research on the fungi as the announcements, one quickly following the other, of the discovery of nuclear fusions in the teleutospore, in the ascus, and in the basidium. Dangeard and Sappin-Trouffy (9) first learned in 1893 that in the teleutospores of *Puccinia buxi* there are originally two nuclei, which unite as the spores come to maturity. This was an important discovery and highly interesting at that time, because it suggested the working out of a process of sexual reproduction. What is the real nature of these two nuclei? Where do they come from? At what time does the transition from the haploid to the diploid condition take place? In our desire to find the answers to these questions, have we not some of us been inclined to under-estimate the importance of Dangeard's original discoveries?

Cytological studies on the rusts since 1893 have resulted in the accumulation of much knowledge regarding the essential features in the life history of a number of species. It ought to be profitable to take stock of this knowledge to see what it may tell regarding the nature, the origin, and the relationships of the rusts, or more particularly at this time what it tells us about their sexuality. Wholly aside from the purely academic question as to the propriety of calling cell fusions or nuclear migrations sexual processes, and the cells or nuclei involved gametes, any discussion of sexuality in this group appears in some way to lead to a consideration of that inherent nature of the rusts to develop so erratically, yet so characteristically, in different types of life cycles.

We interpret what we see recurring in one group of plants in the light of what that would mean were the same thing observed in some other group believed to be related in its phylogeny. We choose to view today the picture of the rust life cycles against the background of a red alga ancestry

Whatever may have been the origin of the Uredineae there are several features in the Florideae which afford a basis for making certain deductions with respect to the sexuality and, therefore, origin of life cycles in the rusts. In the Nemalionales after fertilization, there appear outgrowths from the carpogonium in the form of sporogenous filaments, very short in the simplest forms, long and branched in others. Haploid carpospores are formed and the cycle is repeated.

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[1] Presented before the International Congress of Plant Sciences, Section of Mycology, Ithaca, New York, Aug. 20, 1926.

In the long-cycle forms the sporophytic outgrowths from the carpogonium sooner or later fuse with cells specially set apart as auxiliary cells. Sometimes several such cells are involved in these secondary or accessory cell fusions, reminding us of the multiple cell fusions reported by Fromme (16) and others for the rusts. According to Minder (26) in *Choreonema,* a parasitic red alga, the procarpic branches are developed side by side in a sort of conceptacle, with accompanying elongated auxiliary cells; with the fertilization of one egg, the other procarps degenerate, but the auxiliary cells persist and are involved in the multiple cell fusions. Diploid, now, instead of haploid carpospores are formed. If one insists on homologies, no better example could be cited than to compare such specially differentiated fertile fusing cells as one finds in *Melampsora, Phragmidium, Peridermium,* etc. with auxiliary cells in the red algae. This relation is all the more clear when it is realized that in numerous forms of red algae auxiliary cells are also intercalary cells, in multicellular branches, so that they may be either terminal, sub-terminal, or may be surmounted by several cells. In *Puccinia transformans,* the fusing cells are terminal. In *Phragmidium* they are usually subterminal, and in the Peridermiums several cells above the fertile cells become sterilized.

Oltmanns suggests that the morphological sporophyte consists merely of those outgrowths, the sporogenous filaments, which proceed from the carpogonium after fertilization. In the short-cycle as well as the long-cycle forms, then, regardless as to where reduction takes place, the sporogenous filaments alone represent the sporophyte; the tetrasporic plant is an asexual generation, a Nebenfruchtform. Whether or not one accepts Oltmanns' view, it should be held in mind that in the short-cycle rusts, as *Tranzschelia fusca, Endophyllum sempervivi, Crysomyxa abietis, Gallowaya pinicola,* and the long-cycle forms, such as *Puccinia falcariae, P. caricis,* and *Gymnosporangium juniperinum,* after cell fusions there develop sporophytic outgrowths consisting of a series of binucleate cells, in some forms amounting to a branched system of sporogenous hyphae, which may very well be looked upon as comparable to the sporogenous filaments of the red algae. Applying Oltmanns' interpretation to such a heteroecious rust as *G. juniperinum,* the true morphological sporophyte would consist only of the branched system of diploid filaments in the aecidium, the ends of which function as aecidiospore basal cells. In other words, the true sporophyte is still to be looked for on the pomaceous host.

Another feature of the red algae which should be noted is that in certain species tetraspores are developed on the gametophyte. Such anomalies have been a source of much speculation. So far as having any significance with regard to the original type of life cycle in these algae, these examples of reversions should be interpreted just as they should be in the case of the rusts, with great caution.

As Church (8) has very clearly stated the case, it was most likely the monosporangium, which was chosen as the place for reduction in the new diploid phase, which we now call the tetrasporic plant. When for some reason reduction failed to occur, so that diploid carpospores were produced, these spores on germination gave rise to a new plant exactly like the parent gametophytic plant. It may even have developed sex organs, at least it produced monosporangia, which being dip-

loid, were made the seat of reduction. We now call the four daughter spores tetraspores instead of monospores. It is also conceivable that somewhere in the evolutionary series many diploid generations were developed asexually without reduction, the monospores which were cut off being always diploid, and such a form would be represented in the rusts by generations of repeating uredospores. We still have haploid as well as diploid carpospores. Polyspores and pluricellular promycelia are also comparable.

If a plant resulting from the germination of diploid carpospores should produce carpogonial branches—and such cases have been reported—and the egg should develop parthenogenetically, with the outgrowth of sporogenous filaments we should have a form with repeating carpospores comparable to repeating aecidiospores. The beauty of all this is that we have in the Florideae a whole series of irregularities in development exactly comparable to what we are finding in the rusts, with their great aptitude for developing in peculiar types of life cycles.

ORIGIN OF THE BINUCLEATE CONDITION

It is the very diversity of the methods worked out for bringing into a cell nuclei which are destined finally to fuse, that serves most to give us an idea of the true nature of the process.

Nuclear Migration. As neither of the methods heretofore noted had in them the suggestion of a process of sexual reproduction, they were at once forgotten when Blackman (5) announced his discovery of the origin of the binucleate condition by nuclear migrations. Nuclear migration has been found to occur in at least a dozen species of rusts, so that this method must be accepted as one of the common ways of providing for the binucleate condition.

Cell Fusions. Fertilization is brought about in a majority of forms studied by the method first described by Christman (7). Cell fusions are now known to occur in over forty species. In all these cases the fusing cells seem to be more or less specially differentiated, and frequently as in the Peridermiums they are arranged in a palisade layer. In such forms as *Endophyllum sempervivi* (17) and *Puccinia eatoniae* (15) the fusing cells are deeply imbedded in the basal tissue and placed at various angles more or less horizontal.

Anastomoses of Vegetative Hyphae. In *Uromyces alchemillae,* for example, Kursanov (21) notes a nuclear migration into a fertile cell from a purely vegetative cell and Lindfors (22) says that the binucleate condition may arise in this species as the result of fusion between cells of two purely vegetative hyphae, so that in this form alone are found cell fusions between fertile cells, between a fertile cell and a vegetative cell, between two vegetative cells, nuclear migrations of the Blackman type, and practically all intergrading types.

Binucleate Sporidia and Nuclear Division. Early investigators noted that the sporidia in certain species were very regularly binucleate. This fact did not suggest itself very seriously as a solution of the question, for it was realized that aecidia arose from uninucleate mycelia.

Maire (23) thought he had found the origin of the binucleate condition in *Puccinia liliacearum*. He believed that the basal cell became binucleate by the division of its original single nucleus and the subsequent failure to form a cross wall between the daughter nuclei.

Strange as it may seem, it may yet be found that a very large number of rusts begin the binucleate condition with a binucleate sporidium. As noted, Kursanov and Lindfors have found a considerable number of short-cycled microforms, especially those not developing spermogonia, that have a binucleate mycelium throughout the infected region of the host. Neither author has suggested how this condition came about. Lindfors, however, has shown, as it seems, pretty conclusively for one species, *Puccinia arenariae*, that the diploid condition arises as the result of failure to develop a cross wall between each of the pairs of daughter nuclei after the second division in the promycelium, so that a two-nucleate sporidium results. As the entire mycelium is binucleate, Lindfors is convinced that he has the correct explanation in the binucleate nature of the sporidium. This failure to lay down a cross wall in the promycelium is not essentially different from what Maire claimed for *Puccinia liliacearum*, except as to the place where the nuclear division occurs in the cycle. Kursanov is convinced that in *P. rossiana*, the binucleate basal cell does in fact sometimes develop as the result of nuclear divisions and not by cell fusions or nuclear migration. This author has also shown that binucleate aecidiospores of *Puccinia pruni-spinosae* and of *Ochropsora sorbi* may occasionally arise from uninucleate basal cells. The writer (12) has also reported a similar condition as a rare occurrence in *Caeoma nitens*, where binucleate and even plurinucleate spores arise from a basal cell having only a single nucleus.

Origin far back in the Mycelium. Blackman and Fraser (6) hold that in *Puccinia adoxae* and *Uromyces scillarum* the binucleate conditions arise far back from the primordia of the sori. This has been confirmed by Moreau (28) for the last species. Kursanov (21) says of *Puccinia asarina* that after a little growth of the uninucleate vegetative mycelium it becomes binucleate, and that uninucleate mycelium in *Uromyces ficariae* is very rare, possibly only where the mycelium was formed by infection with sporidia.

Life Cycles Wholly Diploid. No cytological work reported since the discovery of the origin of the diploid phase by nuclear migrations and cell fusions has done so much to upset our notions as to the importance of the gametophyte generation and the so-called sexual fusions as the reports by Kursanov and Lindfors that a number of the microforms of *Puccinia* and *Uromyces* go through their life cycles with the entire vegetative mycelium in the binucleate condition.

Kursanov says that even in very young material of *Uromyces gageae* and *Puccinia fergussoni* the mycelium is composed of binucleate hyphae. *P. aegopodii* and *P. arthemisiella* are other microforms in which he found no uninucleate hyphae. Lindfors has added a number of species of microforms to the list of those which have only binucleate mycelium. Besides *P. arenariae*, which is noted elsewhere, he reports the following: *P. albulensis, P. epilobii, P. gigantea, P. saxifragae, P. hol-*

boellii, and *Uromyces solidaginis.* He says that of the 25 microforms he examined he found 13 species had no uninucleate mycelium.

Rust Cycles Wholly Uninucleate. Mme. Moreau (28) was the first to discover that a rust may go through its entire life-cycle with all of its cells, vegetative and reproductive, in the uninucleate condition. She found that there exists in France a strain of *Endophyllum euphorbiae* which develops its aecidia without cell fusions so that the spores are uninucleate. The spore germinates to form a four-celled promycelium and the sporidia give rise to a uninucleate mycelium. Judging from the size of the spore and its large nucleus, and the type of promycelium developed, one may be justified in referring to this strain as having a uninucleated diploid gametophyte mycelium.

Poirault (35) a little later reported that the spores of *Endophyllum centranthi-rubri* also arise from the uninucleate mycelium. In this case there is no question that the gametophyte is uninucleate and haploid throughout. Olive refers to the teleutospores of *Uromyces rudbeckiana* as uninucleate.

Kursanov (21) has found strains of *Puccinia pruni-spinosae* and of *Ochropsora sorbi,* which develop uninucleate aecidiospores of very small size. He has shown that the germ tubes from these spores are uninucleate. Nothing is known as to what kind of a mycelium would arise from infection with these spores. One would think that the uninucleate aecidia reported by Kursanov may belong to a strain which would on infection of the alternate host give rise to uninucleate teleutospores.

The writer has found that a great deal of the orange-rust of *Rubus* is of the type which produces very small uninucleate aecidiospores and which goes through its short cycle wholly haploid. Diploid aecidiospores of this species are much larger.

Miss Mary Brumfield (the writer is much indebted to Miss Brumfield and Professor Fromme, under whom the work was done, for the privilege of discussing her unpublished report at this time) has among other very interesting discoveries found in the *Podophyllum* rust, a race which is uninucleated throughout. The aecidiospores of this race arise without cell fusions from a uninucleated mycelium, each spore thus possesing a single nucleus. The thing to be especially noted is that these uninucleated spores are fully as large as the binucleate spores which she has shown arise as the result of cell fusions. She has pointed out that the nuclei of the uninucleate race are peculiar. The nucleole, which is very distinct, is surrounded by a hyaline area, which sets it off so strikingly from the chromatin masses as to give the appearance of a spore with two nuclei, until it is examined with the oil immersion lens. This race also produces telia with uninucleate spores. The uninucleate teleutospores are likewise about the same size as those having two nuclei and which arise, as she has shown, as the result of nuclear migrations. This uninucleate race of the *Podophyllum* rust and *Endophyllum uninucleatum* have one thing in common: The fact that no matter whether the aecidiospore has one or two nuclei the size of the spore is the same. Neither of the authors has commented on the possible meaning of this fact. These races are especially interesting because of the contrast to be found when they are compared with the uninucleate

race of *Caeoma nitens* (12). When one takes into consideration what occurs in other plants, it does not seem unreasonable to assume that in the rusts we may have apogamous forms which go through their whole life cycle some in a haploid, and some in a diploid condition, with no cell fusions and no reduction divisions.

TYPES OF PROMYCELIA

Until very recently no particular attention has been paid to the form of the promycelium in the rusts. It was not known to indicate anything regarding nuclear behavior beyond the fact that, since it becomes 4-celled, there must always be a nuclear fusion in the spore from which the structure is developed. The one exception noted by Sappin-Trouffy (36) of the formation of a 4-celled promycelium without previous nuclear fusion has been looked upon as presumably an error much like that claim of Maire's (23) regarding the origin of the binucleate condition, and passed by without comment.

There have been references made in the literature to promycelia with other than four cells and with fewer or more than four sporidia. Being considered abnormalities such cases have aroused no interest. Great credit is due the Moreaus (30), who by their cytological work on the promycelia of species of *Endophyllum*, have shown that there is much to be learned by a careful study of these structures.

The Standard Type of Rust Promycelium. The standard type of a promycelium of the rusts and the behavior of the nuclei during its development as determined by Sappin-Trouffy and other cytologists is as follows: The two nuclei cut off in the young spore fuse. The nucleus passes out into the tube and divides heterotypically. In *Coleosporium,* of course, it divides at the place of fusion. The daughter nuclei move apart, become separated by a median cross wall and divide simultaneously; with the formation of additional cross walls the promycelium becomes 4-celled. Of such a type is the promycelium from the teleutospores of *Gymnoconia interstitialis.* Of such a type is the promycelium developed from aecidiospores of *Endophyllum sempervivi.* Quite another type is developed from the aecidiospores of *E. euphorbiae-silvaticae* and from the aecidiospores of the *Caeoma nitens* form of *Gymnoconia interstitialis.*

Promycelia without Nuclear Fusions. As Sappin-Trouffy first held, and as confirmed by Mme. Moreau, the two nuclei in the aecidiospore of *Endophyllum euphorbiae-silvaticae* do not fuse at any time. Kunkel in his report on nuclear behavior in the short-cycle form of the *Rubus* orange-rust, *Caeoma nitens,* states that the two nuclei in the aecidiospore fuse as the spore germinates. In a recent paper by Dodge and Gaiser it has been shown, however, that there are no nuclear fusions in the life cycle of this rust. Inasmuch as the development of promycelia has been worked out perhaps in a little greater detail the illustrations for the second type of promycelium may be drawn from this form.

As the spore germinates the nuclei become pear shaped, elongate and pass into the germ tube side by side, or one preceding the other, and come to lie one ahead of the other at the middle of the tube. Simultaneous, but not conjugate, division

occurs after which the reorganizing pairs of sister nuclei still connected by fibres slip by one another, and a median septum is laid down. In the first type of promycelium each cell of the 2-celled stage contains only one nucleus. In the second type each cell contains two sister nuclei. After nuclear reorganization septa are laid down, resulting in a 4-celled promycelium which can not at maturity be distinguished from a promycelium of the first type. We are led from Sappin-Trouffy's account to infer that the two nuclei in his *Endophyllum* divide conjugately and that pairs of non-sister nuclei pass to each end of the promycelium, and after separating three septa are laid down simultaneously; the Moreaus (30), however, show that the process there is without doubt the same as has been found in the case of *Caeoma nitens*.

Two-Celled Promycelia. Certain strains of *Caeoma nitens* develop aecidiospore chains without cell fusions so that the spores are uninucleate from their origin (12). Nuclear behavior during the formation of the promycelium is the same as it was in the case of the binucleate spores except that as there is only one nucleus to divide the promycelium can have only two cells. There are at least two European species of *Endophyllum* which develop strains with uninucleate aecidiospores, and one of these, *E. centranthi-rubri,* reported by Poirault without details evidently conforms to this uninucleate *Caeoma nitens* type.

The single nucleus becomes pear shaped, elongates, passes through the germ pore and moves to the center of the young promycelium. Here it divides once only and the two daughter nuclei move apart. A median cross wall is then laid down. A sterigmatous growth develops from each of the two cells and a nucleus passes out into each sporidium.

Two-Celled Promycelia, Cells Binucleate. The promycelia formed at the germination of teleutospores of *Puccinia arenariae* (22) are 2-celled at maturity, and produce only two sporidia. Morphologically they are of the same type as those produced by the haploid uninucleate spores of *Caeoma nitens.* Cytologically they give us an entirely different history, as indicating how by the simple process of omitting the two cross walls in the promycelium after reduction divisions, the binucleate condition is maintained in a microform without a subsequent duplication process. The young spores are binucleate and nuclear fusion and reduction divisions occur as in the other type of promycelium developed after nuclear fusions.

Multicellular Promycelia. Multinucleate spores have been reported many times, but their manner of germination had not been followed until the writer undertook to study the germination of such types of spores in *Caeoma nitens.* Moreau (29) states that in the case of the plurinucleate spores of *Endophyllum* the supernumerary nuclei degenerate leaving only two which are presumed to fuse later. This may be true for that species. Giant multinucleate spores are not uncommon in aecidia of the uninucleate strains of *Caeoma nitens.* The germination of these large spores has also been carefully studied (12). Presumably degeneration of nuclei may occur both in the spore and in the promycelium, especially where a large number are originally present. Many cases have been observed, however, where three

or four nuclei pass out of the spore into the large germ tube and there divide once simultaneously.

In this way multicellular promycelia come to maturity. Such promycelia are apt to be branched or double and contain one or more empty or dead cells from which no sporidia have been developed. Theoretically then, if either degeneration or unequal distribution of nuclei does not occur, the promycelium of *Caeoma nitens* should develop twice as many sporidia as there are nuclei in the aecidiospore.

Having seen how the uninucleate spores of *Caeoma nitens* and *Endophyllum centranthi-rubri* develop 2-celled promycelia one may be puzzled to understand how it can be that in the case of *E. uninucleatum*, studied by Moreau, the spores develop 4-celled promycelia. The following table shows comparatively some facts regarding the two strains of *E. euphorbiae* and *Caeoma nitens*:

End. euphorbiae binucleatum

1. Spore binucleate
2. Two nuclei enter promycelium
3. Simultaneous nuclear division
4. A 2-celled stage, two nuclei in each cell
5. Mature promycelium 4-celled
6. Four sporidia

End. euphorbiae uninucleatum

1. Spore uninucleate
2. Spore as large as binucleate spore
3. Nucleus as large as two nuclei of binucleate spore
4. Nucleole large
5. First nuclear division
6. A 2-celled stage, one nucleus in each cell
7. Second nuclear division
8. Mature promycelium 4-celled
9. Four sporidia

Caeoma nitens binucleatum

1. Spore binucleate
2. Two nuclei enter promycelium
3. Simultaneous nuclear division
4. A 2-celled stage, two nuclei in each cell
5. Mature promycelium 4-celled
6. Four sporidia

Caeoma nitens uninucleatum

1. Spore uninucleate
2. Spore small, half the size of binucleate spores
3. Nucleus same size as those in binucleate spore
4. Nucleole small
5. One nuclear division
6. Mature promycelium 2-celled
7. Two sporidia

It should be noted that in its development and nuclear behavior the promycelium of *Endophyllum uninucleatum* corresponds exactly with those formed from spores in which there has been a nuclear fusion. If this strain had been derived from *E. sempervivi*, where a nuclear fusion occurs in the spore, we might well assume that it was derived as the result of two divisions in the promycelium without actual reduction. Among the apogamous ferns, it is well known that we may have strains of species that go through their life cycle gametophyte and sporophyte in some cases in the haploid, in others in the diploid condition. On the assumption that Mme. Moreau has all the facts in this case we are inclined to view these large spores with large single nuclei as diploid, having become so by chance nuclear fusions in the parent form where usually no nuclear fusion occurs. In such an event a uninucleate race would evolve, devoid of cell fusions, since each nucleus in the entire mycelium is already diploid, the promycelium having gone through the form of reduction without chromosome reduction.

This is not an unheard of phenomenon. Wingard (40) has proved conclusively in case of the yeast-like Ascomycete, *Nematospora*, that the ascus nucleus goes through the form of a double reduction, three successive divisions, though there have been no nuclear fusions in the whole life cycle. There can be no question of the facts here since asci may bud out directly from ascospores.

In those basidiomycetes such as the strain of *Camerophyllus* (4) without clamp connections, where the young basidium is uninucleate and no nuclear fusions occur in the life history, the nucleus enlarges and goes through the form of synapsis just the same as if it were beginning the reduction divisions.

Kniep (18) has shown that in cultures of *Armillaria mellea* the basidia may arise directly from a uninucleate mycelium. There is no nuclear fusion in the basidium yet the primary nucleus divides twice, going through synapsis and diakinesis. Four sporidia are developed on the basidium. It goes without saying that unless nuclear fusion takes place somewhere in the life history, perhaps at an early stage after the germination of the spores, such divisions could not be in fact reduction divisions.

REPEATING AECIDIA

Meinecke (24, 25) has twice reported on series of infection experiments covering several years which prove conclusively not only that there is a strain of *Peridermium cerebrum* on the Pacific Coast that is short-cycled, but that the pine can be repeatedly infected by sowing aecidiospores which develop typical, long germtubes. It is interesting to note in this connection that no spermogonia have been found on the galls, otherwise this strain of the rust can not be distinguished from the aecidial stage of the heteroecious strain of *P. cerebrum* of the east, which readily infects oaks. Cytological work, now under way, may serve to further clear up two very interesting questions—first, that of unstable rusts, and, second, that of repeating aecidia. If, in case of repeating aecidia, we should have a binucleate mycelium without spermogonia, you might call the diploid mycelium gametophytic, because it represents morphologically that generation which usually gives rise to spermogonia, and it may be compared to a diploid prothallium which produces the sporophyte apogamously. The aecidium is normally sporophytic.

Uromyces scrophulariae is a species with repeating aecidia. Kursanov (21) says that the primary mycelium resulting from infection by sporidia is generally binucleate, but one also finds in places hyphae purely uninucleate. The spermogonia are formed from uninucleate hyphae, but the aecidia which appear at this time are formed from two kinds of hyphae, binucleate and uninucleate; most of the aecidiospores develop from the binucleate hyphae directly. In addition there occur fusions between equal uninucleate cells from which there develop chains of spores. Infection experiments show that teleutospores develop from the same primary mycelium a little after the aecidia and from only binucleate hyphae. Infections with aecidiospores result in formation of aecidia and telia, but no spermogonia.

CELL FUSIONS AND NUCLEAR MIGRATIONS,—SUBSTITUTES FOR SEXUAL FUSIONS

For Dangeard the fusion of the two nuclei, the diplogametes in the teleutospore, constitutes fecundation, and the cell in which the nuclear fusion occurs is

the egg. In *Puccinia buxi* the gametophore, as Dangeard calls it, is binucleate; it is inserted on a pair of pseudogametangia, which furnish two nuclei. These two nuclei undergo one or two divisions only, before furnishing the two nuclei of the diplogametes. Nuclear fecundation gives a 2n egg. Reduction takes place on the germination of the egg. Moreau (27) carries Dangeard's idea further, denying that the cell fusions are sexual fusions. She recalls examples of how the binucleate condition arises in different ways in the fungi. Moreau says if you call cell fusions in the rusts sexual fusions, then all the other ways of bringing about duplications of the nuclei must likewise receive the same interpretation, which is absurd.

Without accepting Dangeard's conception that the teleutospore is the egg, Kursanov (20) has pointed out why we should look upon the various ways by which the rusts change from the haploid to the diploid condition as merely substitutes for the sexual fusion of gametes. Most students of the nuclear phenomena in the rusts, however, have followed Blackman and Christman in the use of the terms sexual fusions and gametes.

Sterile cells above the fertile fusing cells are not trichogyne homologues. Such terminal sterile cells are developed in secondary uredo sori, *Puccinia iridis* (20), and in telia of species of *Gymnosporangium* (11) whereas in the Caeomas and Peridermiums (1) their nature as purely space-making buffer cells can not be questioned.

If the cells which fuse are not sex cells, what are they? In view of the frequent development in the red algae of definite and morphologically distinct auxiliary cells, which become involved after fertilization in all sorts of cell fusions, it has been suggested (13) that where you have specifically differentiated fertile cells as in the Caeomas, they may be homologized with the auxiliary cells of the red algae. In this connection it would be unscientific to speak of them as sex cells or gametes and the fusions as sexual fusions. They are simply substitute fusions of vegetative cells.

Some ferns are recognized as apogamous because they develop without the functioning of gametes. In *Lastraea* (14) nuclei from two adjacent vegetative cells of the prothalium fuse. In *Aspidium falcatum* (2) sixteen spore mother cells use in pairs followed by nuclear fusions. No one has referred to such fusions as sexual fusions, although normal sporophytes develop after such vegetative fusions.

In the heterothallic Ascomycete, *Ascobolus magnificus* (10), you first must have vegetative cell fusions, anastomoses of hyphae, then you must have sexual fusions between sex cells; after this you may have cell fusions of a third kind before the ascus arises. Finally, there is the nuclear fusion in the ascus. All three sets of fusions are essential to the maturity of an ascus, only one fusion being sexual. In the heterothallic species of *Coprinus* an anastomosis of hyphae from the compatible strains is essential. Yampolsky (41) has recently pointed out that all plants can not be classed as either monoecious, dioecious, or hermaphroditic. There are at least twenty different kinds of oecisms. Sexual reproduction does not occur in the Basidiomycetes, and we should not refer to a *Coprinus* as having two sexes, four sexes, or maybe some day as having twenty sexes.

INTERMINGLING MYCELIA

Perhaps no phase of the cytology of the rusts has caused so much uncertainty and speculation regarding the nature of rusts as the work on the intermingling gametophytic and sporophytic mycelia. The unpublished work of Miss Brumfield referred to at another place in this paper will no doubt serve to clear up much of the uncertainty as to the real course of events in *Puccinia podophylli,* and thus stimulate a reinvestigation of such forms as *Puccinia suaveolens, Gymnosporangium bermudianum,* and other species in which there has been reported intermingling of haploid and diploid mycelium. It should be pointed out that Mme. Moreau (27) in her study of *Uromyces ficariae,* after two previous authors had reported that the binucleate condition arose very early at some indefinite point in the mycelium claims that the binucleate condition arises in a perfectly regular manner by cell fusion at the base of the telium. In spite of this report, however, Kursanov later (20), in the main, upholds Blackman and Fraser (6) in their view that there is but little growth of the uninucleate mycelium. He was unable to find any evidence of cell fusions in the sorus primordium.

Lindfors (22) thinks he has the solution of this puzzling question of intermingling mycelia. He believes that in *Uromyces alchemillae,* for example, most of the mycelium is haploid in its real nature, although many of the cells may contain more than one nucleus. He says this is no doubt due to the failure to lay down cross walls after nuclear division. This would be very likely to happen in the rapidly growing tissues of the host where the mycelium would be stretched. As further evidence, he refers to the development of the mycelium of *Puccinia glumarum.* The germ tubes, substomatal vesicles, and hyphae growing from them are at first multinucleate, and much of the mycelium is made of plurinucleate cells. It is only in the vicinity of the sorus primordium that the binucleate condition becomes regular. He thinks this becomes so by the inclusion of two nuclei in each cell as the septa are laid down. The cell may become binucleate, he also thinks, by the degeneration of supernumerary nuclei. Such an irregular system of growth would hardly fall in line with the much exploited theory of dikaryons for the so-called sporophyte mycelium of the rusts, where the paired nuclei are supposed to divide conjugately throughout the sporophytic stage. If one searches the literature, he finds a great deal of assumption, but no proof, that such is the method of nuclear division in the mycelium. One finds no definite or positive statements denoting first hand knowledge of conjugate divisions in vegetative hyphae of any rust. It would be interesting to know just how in any such form as *Puccinia glumarum* the dikaryon becomes established as extensions of multinucleate substomatal vesicles and plurinucleate hyphae.

CONJUGATE NUCLEAR DIVISION

Olive (33) describes simultaneous division of nuclei in certain multinucleate cells in the rusts, but the evidence offered has no bearing on the development of the dikaryon. Sappin-Trouffy (36) figures diagramatically what are in reality simultaneous nuclear divisions, but which may be interpreted by some as conju-

jugate divisions, in the germ tubes from aecidiospores and uredospores. Purely con-
jugate divisions are so manipulated as to cut off non-sister nuclei in the new cell.
Nothing of the kind occurs in the case of those divisions figured by Olive and
Sappin-Trouffy as conjugate divisions. If conjugate divisions always take place in
the growth of the dikaryon system of the rusts, it is strange that they should not
have been seen and figured. Kursanov followed particularly hyphae of *Puccinia
suaveolens* for eight consecutive cells without finding evidence of conjugate divi-
sions. Some of the results of his observations, showing the number of nuclei in
adjacent cells follow: 3-1-2; 2-2-2; 3-2-2-2-1; 2-3-3-3-3-2-2; 2-2-1; 3-0-2-1; he
did not observe more than three nuclei in any one cell. In view of such irregulari-
ties it looks as though we shall be compelled to give up some of our ideas regard-
ing the fixity of the dikaryon or of the haploid and diploid conditions, and accept
the situation as it is, realizing that it is the general morphological structures and not
the behavior of nuclei in particular cases that ultimately must be our guide in
interpreting life cycles of the rusts.

TELEUTOSPORES IN AECIDIA

Whether the occurrence of teleutospores in aecidia always is due to the same
cause or means the same thing from the standpoint of the origin of life cycles may
be questioned. Jackson has reported that in a tropical species of *Endophyllum*
which he studied the walls of the aecidiospores are becoming so much thickened
as to suggest to him that this form is in the process of changing its aecidium into
a telium. Arthur and Fromme (3) note that in *Endophyllum tuberculatum* one
finds in any mount of aecidiospores some two-celled teleutospores The genus
Pucciniosira is interesting in this connection as possibly showing the trend of evo-
tion. Certain species develop chains of two-celled teleutospores. In *Endophyllum
sempervivi,* as Hoffman has noted, the cell fusions take place well down in the
aecidium primordium. Perhaps as a result of this, there are developed short chains
of binucleate cells from the fusion cells before the basal cells are organized. A
cytological study of an American form of *E. sempervivi* gives us a hint of the nature
of the two-celled spores of the Endophyllums, spores which have much the appear-
ance of being teleutospores. If they are true teleutospores their method of develop-
ment in *Endophyllum* ought to mean that the telium has been evolved from the
aecidium. Frequently with the division of the aecidiospore initial a very large
intercalary cell is cut off. Instead of disorganizing, as do most intercalary cells,
its nuclei and cytoplasm persist, the cell increases in size, remaining attached to
its companion aecidiospore cell. Sometimes only one pair of such cells mature in
a chain. The supporting basal cell and the one or two additional binucleate cells
beneath degenerate. When this happens the pair of cells, consisting of intercalary
cell and aecidiospore attached to the disorganizing remains of the binucleate cells
referred to, certainly simulate a two-celled teleutospore. There is no reason why
a promycelium may not develop from such an intercalary cell. Unless, however,
it is admitted that the teleutospores from such a form as *Puccinia graminis* were
likewise evolved from aecidiospores and intercalary cells, these two-celled spores of
Endophyllum should be recognized for what they are rather than as teleutospores.

SPERMOGONIA

The importance of giving due consideration to the question of the presence or absence of spermogonia should not be overlooked. While no one would contend that in the rusts known today the spermatia function in fecundation, they still must be recognized as sex organs, and as such prove by their presence the existence of a sexual element in the mycelium bearing them. As Dodge and Gaiser (13) pointed out, the same potentiality of a rust mycelium to develop spermogonia may be the very thing that is the essential stimulus to cell fusions and nuclear migrations. Kursanov repeatedly calls our attention to the absence of these structures in such forms as *Uromyces alchemillae*, *U. ficariae*, *U. gageae*, *P. fergussoni*, *P. asarina* and *P. artemisiella* where the binucleate condition arises at indefinite points, or where the entire mycelium is binucleate. Lindfors (22) found that in thirteen out of twenty-five microforms studied the entire mycelium was binucleate,—no cell fusions, no nuclear migrations. *Puccinia arenariae*, *P. albulensis*, *P. epilobii*, *P. gigantea*, *P. saxifragae* and *Uromyces solidaginis* are among those which have no spermogonia. *Puccinia adoxae* and *Uromyces scillarum*, microforms without spermogonia, studied by Blackman and Fraser (6) and by Moreau (27), are known to develop the binucleate condition very early in the vegetative hyphae. Strains of *Caeoma nitens* without spermogonia develop uninucleate aecidiospores without cell fusions.

COMPOSITE LIFE CYCLES

Uredinologists have long been aware of the existence of a number of species of short-cycle rusts which by host relations or morphology seem to indicate that they are correlated with certain long-cycle forms. In other species the development of telia and aecia close together has been of special interest because of the suggestion of the possibility that both forms of sori may arise from the same mycelium. Whetzel (39) was the first, however, to show conclusively that a species may in fact have two distinct life histories, or be able to go through two different life cycles independently. *Puccinia podophylli* lives for a time as a micropuccinia, then later becomes long-cycle, developing aecidia and, by secondary infections, telia. Miss Brumfield has shown that spermogonia, aecia, and telia may develop side by side from the same mycelium from the early spring infections. This mycelium is essentially gametophytic and usually the aecidiospore chains arise from cell fusions. The primary teleutospores from the same uninucleate mycelium arise after nuclear migrations.

Perhaps *Uromyces acetosae* described by Lindfors (22) has a similar composite life history. He finds telia frequently develop near aecia and apparently from the same uninucleate mycelium. He was unable to determine how the basal cells become binucleate, but assumes that duplication takes place somewhere in the base of the primordium. The writer (12) has reported and has under observation several cases of infection of blackberry by a peculiar strain of orange rust. In certain sori part of the aecidiospores develop promycelia and the other part germ tubes, functionally showing a composite life history.

CONCLUSIONS

The spermatia of the rusts are male sex organs and when present indicate that the species has in it the male element of sexuality and as such functions in a secondary way.

There is no structure in the rusts comparable to the procarpic branch, therefore, no organ that can be homologized with the egg or trichogyne.

"Fertilization" is accomplished in the rusts by various methods. Cell fusions, nuclear migrations, hyphal anastomoses or any of the other known methods by which the binucleate condition is attained, are not sexual fusions and the cells or nuclei involved are not sex organs or gametes. There are no cases of sexual reproduction known in the rusts.

If homologies are insisted on, it may be suggested that the auxiliary cells and the secondary or accessory cell fusions which follow after fertilization in the red algae may very properly be compared to those specifically differentiated fertile cells and cell fusions of the rusts.

All plants were not cast in one mould; the algae and fungi were not created to serve as illustrations for a beautiful theory of evolution based entirely on the scheme of alternation of generations; as applied to the algae and fungi this is a scheme used by overworked school teachers to furnish busy work for their students.

Nuclear condition, or nuclear behavior, is not the criterion by which the gametophytic and sporophytic phases are delimited.

A proper conception of the application of these terms in the red algae and rusts and a clear notion of the meaning of sexuality and sexual reproduction as contrasted with substitute processes is essential to the understanding and appreciation of life cycles in the rusts.

Oltmanns' suggestion that the sporogenous outgrowths from the fertilized egg in the short-cycle and the long-cycle red algae, regardless of where reduction takes place, represent the morphological sporophyte and that the tetrasporophyte is merely a "Nebenfruchtform," should be given consideration. In the heteroecious rusts like *Gymnosporangium juniperinum*, if again homologies are demanded, the separation of the two phases, gametophyte and sporophyte, is not brought about with the alternation of hosts. The branched systems of binucleate hyphae extending from the point of duplication to the aecidiospore basal cells are just as much the sporophyte as the binucleate mycelium in the teleutospore host, perhaps even more so.

"Fertilization" may be accomplished by cell fusions without nuclear fusions and by nuclear fusions without cell fusions.

Rust life cycles are not necessarily fixed.

A rust may go through its particular life cycle without either cell or nuclear fusions.

A rust, so far as its vegetative mycelium is concerned, may go through its cycle wholly haploid or wholly diploid.

A rust may fulfill its destiny wholly uninucleate, yet still be wholly diploid, and vice versa.

Types of promycelia are valuable criteria for judging preceding nuclear behavior; cytologists should see and figure more promycelia.

Cells of gametophytic hyphae may be uninucleate, binucleate, or plurinucleate; cells of the teleutosporophyte may be plurinucleate. No one has ever shown that the binucleate condition is maintained in the vegetative mycelium by conjugate nuclear divisions.

The occurrence of aecidiospores or peridial cells in a telium or of teleutospores in an aecidium merely by their presence tell nothing of the workings of evolution.

The Whetzel method of studying *Puccinia podophylli,* if supplemented by cytological work based on pedigreed cultures, will go far to solve the mysteries surrounding other forms with reputed mixed mycelia.

The rusts, higher basidiomycetes, and ascomycetes, are closely related groups evolved from the red alga line. Long cycle rusts are more primitive.

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PHYSIOLOGIC SPECIALIZATION AND SPECIES DEVELOPMENT AND NOMENCLATURE[1]

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It is generally agreed that the rusts are very closely adjusted to their hosts. So far no one has been able to grow their mycelium upon an artificial substratum. They require living host plants and their best development occurs when such hosts show vigorous development. The rusts not only require living plants but show marked specialization to certain hosts. As a group, their hosts are found only among species of the Pteridyphytes and Spermatophytes. Usually, the various species of rusts are found on more or less closely related hosts. Even when classified strictly upon a morphologic basis, rust species differ markedly in the range of hosts upon which they are collected, some species being restricted to only one species of host while others have been considered as infecting species in many genera and in some instances in a number of families. As the result of the extensive studies of Eriksson, followed by the investigations of numerous other workers, it is now apparent that within these morphologic units there are groups which differ from each other in the hosts within which they will develop. These groups also differ markedly in their choice of hosts. In some cases they are restricted to a few varieties or even strains of varieties of species while in other cases they may find congenial hosts among varieties or strains of species of a number of genera although other strains of these same species are unfavorable for their development. By culturing the rusts to a series of strains or varieties of species it has been found possible to distinguish groups among the morphologic units of the rusts with as great or greater accuracy than that used in distinguishing such morphologic units. The number and characterization of such groups depend upon the number and variety of host plants employed in such studies. Thus Eriksson, using a series of grass species including wheat, rye, oats, etc., was able to distinguish a number of races in stem rust of the grasses, *Puccinia graminis*, a race *tritici* being distinguished by its ability to infect certain species of *Triticum* as contrasted with inability to develop on species of *Secale* and *Avena*. Stakman and Levine in their studies of this race *tritici* have shown that by using a set of eleven varieties of *Triticum*, thirty-seven physiologic forms of stem rust of wheat can be distinguished by differences in reaction of these varieties. It is probable that if a more extensive set of varieties of wheat had been used, some of these forms would have been found to be made up in turn of several forms

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distinguished by the additional wheat varieties. There are, therefore, among at least some of these morphologic groups or species of the rusts, a number of varieties, races, strains, forms, lines, whatever one may want to call them, which differ from each other in adaptability to varieties, strains or lines of phanerogamic species.

Just what the condition or conditions are which determine this adaptability is for the most part unknown. As has been indicated, in some cases it is to be found in a number of host species. In other cases such conditions are to be found in certain varieties of a few species. Even strains of such uniform morphologic groups as agronomic varieties may differ markedly in those factors determining susceptibility to rust. While the nature of the factors determining adaptability is unknown, genetical studies have shown in a number of cases that resistance or immunity of a given variety or line to rust is inherited as a simple factor.   In some cases, it is probable that a number of factors are responsible. Since it has been found that resistances of two different varieties to different physiologic forms are separately inherited as simple factors, it would appear that the nature of the resistance in the two cases is different. Since a rust and its host are two interacting organisms their adaptability is determined by the presence or absence of compatible factors on each side. With a number of such factors involved there exist possibilities of different combinations which may explain the number of physiologic forms in some rust species and the hosts which are favorable for their development.

The part which host specialization plays in the development of rust species cannot be stated with any great degree of certainty. Since for a considerable portion of their development the rusts are restricted to living plants, it is natural to expect that the host-environment has played a considerable part in their phylogeny. The rusts are obviously very closely adjusted to their hosts. Those factors which result in producing evolution in the latter are likely to bring about changes in the parasite. It is evident that where the evolutionary changes produced in the host are such as to adversely affect the balance between the host and rust, there will tend to be an elimination of the parasite unless a corresponding adjustment takes place in the rust. It is possible that plasticity of hosts has also found reflection in plasticity in their rusts. Where host species are evolving rapidly, groups are produced consisting of a large number of intergrading, gradually diverging species. This may find reflection not only in their morphologic character, but in their physiologic functions as well. The rust parasites meeting such conditions are carried along on the diverging host lines in some cases with differentiation in morphologic characters and a number of morphologic distinguishable groups or species are formed. It has been noted by a number of investigators that in such groups as the Rosaceae, Carduaceae, Cichoriaceae, Umbelliferae, etc., where there are numerous intergrading species, the rust parasite also tends to show a corresponding number of intergrading species. When the host species met unfavorable conditions and perished, in many cases the corresponding rust group was eliminated, and there resulted both host species and rust species sharply delimited morphologically from each other and probably in most cases also physiologically. In other cases

there was no morphologic differentiation in the parasite to correspond with the evolution of host lines and in consequence a rust group of similar morphology, a species, is developed upon more or less distantly related and distinct hosts. There may have been physiologic differentiation, however, to meet corresponding developments in the various host species and within the rust species distinct physiologic groups were evolved. The possibilities are so numerous that it is not much wonder that a bewildering complexity of morphologic and physiologic grouping has resulted.

Just how such evolutionary changes have been brought about must be largely a matter of speculation. This is even more true of the rusts than of their hosts, since so little is known concerning many of the fundamental functions in the rusts. There are so many questions which are unanswered. Is the pycnium a functionless, vestigial male organ? If so, what is the importance of the cellular fusions at the base of the aecium? Do crosses occur between forms of the rusts? Do mutations occur? These are important questions not only in connection with the phylogeny of the rusts, but also in connection with their control. If the pycnium is actually a functionless male organ, it may be that crossing is now impossible in the rusts and evolution and development of new forms by hybridization may now be impossible. On the other hand, through the fusions at the base of the aecium crossing between rusts may still occur and new forms may be arising in this way. Can a similar result also be produced by the anastomosing of hyphae recently reported by Dr. Allen?

Concerning the stability of rust forms, there is some experimental evidence, although investigators by no means agree. Ward, Pole Evans, Long, and others have claimed that the parasitic capabilities and even morphologic character of the rusts may be changed by growing them on certain species of hosts, the so-called bridging species. In these investigations unfortunately there is an uncertainty concerning the purity of the rust cultures which were employed. Stakman and co-workers in their investigations of *Puccinia graminis* have been unable to find any such change. If through bridging species the parasitic nature of the rusts may be changed it is easy to conceive how the rusts kept pace with the evolution of their hosts. More critical evidence is necessary, however, before such conclusions can be drawn.

Host specialization has almost from the very beginning played a more or less important part in the nomenclature of the rusts. At least, following the realization of the obligate parasitism of the rusts, there has been a tendency to group into species those rusts upon closely related hosts. The investigations of Eriksson showed that even on closely related hosts, rusts of similar morphology showed a marked difference in their selection of hosts. In some cases the differences in specialization between such forms were even more pronounced than the morphologic distinctions used to separate species. For this reason some investigators have considered that such sharply specialized groups should be separated and designated as species. The usage has not been at all uniform. Some investigators have differentiated rust species largely by morphologic characters, subdividing such

species according to their host specialization into groups variously designated as varieties, races, biologic forms, physiologic forms, etc. In heteroecious rusts, some workers have considered that while specialization in the sporophytic phases indicated races, specialization in the gametophytic phase is sufficient for distinguishing such groups as species. Some of the criteria employed in other groups to distinguish species are hardly feasible among the rusts. Nothing is known concerning hybridization in the rusts. Until crosses have been obtained it is not possible to apply this as a species test. Provided crossing occurs, the host specialization of the rusts presents a difficulty in some cases where rusts do not have a common host for gametophytic phases.

There is no question that in many cases the sharp and apparently well fixed specialization of forms of rust to certain hosts can be used to readily distinguish such forms from others of closely similar morphology. Whether such distinctions alone are sufficient to justify the species designation is questionable. While physiologic forms of rust can be distinguished by their ability to parasitize strains of wheat, strains of agronomic varieties of wheat can also be distinguished by their reaction to certain physiologic forms of rust. If such rust forms are to be considered species, should not similarly distinguishable wheat strains also be considered species? Would this not lead to the species concept advocated by Lotsy according to whom a species is "a group of individuals of identical constitution unable to form more than one kind of gametes?" Is it possible to distinguish rust "species" on any such basis? Certainly none of the groups now recognized can unquestionably be considered species on such a basis. Is this not designating a pure line in the strict sense, a species? In the rusts, at least, is there anything to be gained by such a change? Why call a pure line a species and then unite such into a group showing similarity of morphology and employ some other term such as Linneon instead of the term species?

With our present knowledge of the rusts they may be variously grouped, according to life cycle, according to morphologic similarity, according to whether this or that species, variety, strain, etc., is a favorable host. They all serve to distinguish groups with certain characteristics in common. It is questionable whether there is anything to be gained by applying a specific name to each of the divisions and subdivisions which are distinguishable with more intensive study from different points of view. It would appear less confusing to retain the specific name for those groups distinguishable by morphology and life cycle and indicate by other means the sub-divisions according to various reactions.

GENERAL PROCEEDINGS

INCEPTION OF THE CONGRESS

A general statement describing the inception and early organization of the International Congress of Plant Sciences has been published,[1] and it is perhaps unnecessary to repeat more than a few statements made in the previous announcement.

At representative meetings of American botanists (Botanical Society of America, American Phytopathological Society, Ecological Society of America) held in Cincinnati, December, 1923, a proposal suggesting the desirability of holding an international congress for all workers in the fields of the plant sciences (botany in its widest applications) was enthusiastically approved.

In making the proposal it was clearly recognized that in view of preparations made, and then necessarily abandoned, for a Fourth International Botanical Congress in London in 1915 (as authorized by the executive committee of the Brussels Congress, 1910), the British botanists enjoyed, if they wished to exercise it, a prior claim in respect to such arrangements. Further, there were endorsed by the three societies mentioned suggestions that if at the present time British botanists did not wish to undertake arrangements on British soil for such a congress, but would be willing or would prefer to have the initiative taken in the United States, then American botanists would gladly undertake to bring about an international gathering at a date as early as might seem practicable. Representing the three societies, there was appointed an organizing committee consisting of H. C. Cowles (Ecological Society), B. M. Duggar (Botanical Society) and H. H. Whetzel (Phytopathological Society). This committee was authorized to ascertain the wishes of British botanists, and if a favorable sentiment was manifest toward convening the congress in the United States, to proceed with the necessary arrangements.

Communicating with one of the presidents and with the secretary representing the proposed congress in London, in 1915, it seemed that the initiative might well be taken by American botanists.

Letters were received from Professor F. O. Bower and Dr. A. B. Rendle, representing the executive committee of the proposed London Congress, also a letter from Mr. F. F. Brooks, Secretary of the Imperial Botanical Conference; all of these clearly indicating that there would be no objection on the part of British botanists to the proposal.

In due time the organizing committee received assurances of the cooperation of the various American research societies in the plant sciences and accordingly proceeded with plans for an international congress, promptly formulating the following general regulations and tentative schedule.

1. An International Congress of Plant Sciences (Fourth International Botanical Congress) shall be held in Ithaca, New York, August 16-23, 1926.

2. Membership in the congress shall be unrestricted and conditional only upon subscribing to any regulations announced and upon the payment of such nominal fee as may be necessary for legitimate expenses in organizing and conducting the congress.

3. In the scope of the congress shall be included the different branches of botanical science together with what are known as its broader applications in the fields of bacteriology, agriculture and forestry—these various aspects to be suitably grouped in sections. To the end that this characterization may be effective and practically inclusive, the cooperation of all the

[1] Science, N.S. 61: 58-59. Jan. 16, 1925.

special American societies that may be interested in the general arrangements shall be solicited and urged.

4. The work of the congress shall be primarily with problems of fundamental research and teaching, but adequate opportunity shall be accorded all sections for the discussion of regulatory recommendations of international significance.

5. Ample time shall be reserved in the preparation of the program for excursions of interest to the various sections.

6. Particulars of the meetings, discussions and excursions shall be published as early as practicable.

Every available source of publicity was utilized in making known the character and time of the Congress to botanists throughout the world. Circular letters were also mailed to all botanists listed as members of national societies and organizations, the lists of which were available to the secretary.

The date arranged for the congress was selected after taking into consideration a variety of circumstances affecting both the place of meeting and the convenience of those attending from far and near. All conditions seemed as favorable as could be anticipated, though it was clear that conditions in Europe would make it difficult for many to attend who might, under other circumstances, have found it possible to do so.

ACKNOWLEDGMENTS

The work of the Congress was greatly facilitated through the cooperative interest of the Division of Biology and Agriculture of the National Research Council, and this assistance is gratefully acknowledged. The officers and the organizing committee record with special gratification the courtesy of Cornell University, through President Livingston Farrand, in permitting the use of its facilities for the Congress, thus assuring a convenient geographical location and a most favorable physical environment. The Congress is under many obligations, not alone to Cornell University, but also to many members of the faculty and the many citizens of Ithaca for their generous assistance and cooperation. It is, further, a privilege to express the thanks of the executive committee to those who willingly assumed the responsibilities of patrons, similarly to those professionally interested who likewise contributed to the financial and other needs of the work of the organization.

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Ecuador: Wilson Popenoe.

Germany: University of Tübingen: E. Lehmann.

Great Britain. British Association for the Advancement of Science: A. B. Rendle, A. W. Hill; British Museum of Natural History: A. B. Rendle, J. Ramsbottom; Royal Botanic Gardens, Kew: A. W. Hill, T. A. Sprague, Miss E. M. Wakefield; The Royal Society, London: E. J. Butler, A. W. Hill, A. B. Rendle; Technical College of Huddersfield: T. W. Woodhead; University of Bristol: B. T. P. Barker, T. Wallace (Agricultural and Horticultural Research Station); University of Cambridge; A. W. Hill, A. G. Tansley; University of Durham: Kathleen B. Blackburn; University of Edinburgh: George W. Scarth; University of Leeds: W. H. Pearsall; University of London: A. G. Tansley.

India. Indian Botanical Society: L. A. Kenoyer.

Italy. Citrus Experiment Station, Acireale, Sicily: Giulio Savastano; International Institute of Agriculture, Rome: Alessandro Marcello, R. A. Oakley.

Japan: K. Shibata; Kyushu Imperial University, Fukuoka: T. Koyama; Tokyo Imperial University: K. Shibata.

Mexico: Manuel Mesa A.

Netherlands: F. A. F. C. Went, H. M. Quanjer, E. van Slogteren; Netherlands Botanical Society: F. A. F. C. Went, M. J. Sirks; Royal Academy of Sciences, Amsterdam: F. A. F. C. Went.

New Zealand. University of New Zealand: John Charles Sperrin-Johnson.

Philippines. University of the Philippines: Arthur F. Fischer.

Poland. College of Agriculture, Warsaw: Feliks Kotowski; Polish Academy of Sciences: W. Szafer; Polish Ministry of Public Instruction: W. Szafer.

Porto Rico: J. A. B. Nolla, R. A. Toro.

Roumania. University of Clug, Roumania: A. Borza.

Spain: Fernando Silvela Tordesillas; Royal Academy of Sciences, Madrid: Henry A. Pilsbry.

Switzerland: John Briquet, Eduard Rübel; Botanical Garden of Geneva: Eduard Rübel, John Briquet; Society of Physical and Natural History of Geneva: Robert Chodat; Swiss Experiment Station for Horticulture, Wädenswil: G. Jegen; University of Geneva: Robert Chodat.

Sweden: Nils E. Svedelius; Swedish Royal Academy of Science: Nils E. Svedelius; University of Upsala: Nils E. Svedelius; The Gothenburg Botanical Garden: Carl Skottsberg.

Union of South Africaä A. M. Bottomley.

United States of Soviet Russia. Academy of Sciences, Leningrad: V. Lubimenko; All Russian Institute of Applied Botany and New Cultures, Leningrad: N. Maximow, T. Maximow; Russian Department of Agriculture: B. L. Issatchenko; Scientific Institute of Lesshaft, Leningrad: V. Lubimenko; State Institute of Agriculture and Irrigation, Novocherkassk on Don: B. A. Shumakov, E. A. Zemchuznikov.

United States. American Academy of Arts and Sciences, Boston: B. L. Robinson; Biological Society of Washington: S. F. Blake, A. S. Hitchcock; Carnegie Institution of Washington: Charles B. Davenport, Albert F. Blakeslee, H. M. Hall; Connecticut College: Caroline Black, Evelyn Fernald; Elmira College: Elizabeth L. Whittaker; Goucher College: Ralph E. Cleland; Mount Holyoke College: Anna M. Starr; New York Academy of Sciences: N. L. Britton, R. A. Harper, H. M. Richards; New York Botanical Garden: A. B. Stout; Oberlin College: Frederick O. Grover, Susan P. Nichols; St. Lawrence University: Constance Hartt; Stanford University: LeRoy Abrams, Gilbert Morgan Smith; State College of Washington: Harold St. John; Torrey Botanical Club: Arthur H. Graves University of Arizona: J. J. Thornber; University of Chicago: Henry C. Cowles; University of Hawaii: Herbert F. Bergman; University of Illinois: William Trelease; University of Minnesota: Henry Schmitz, Raphael Zon, A. H. Larson, J. Arthur Harris, H. K. Hayes, A. T. Henrici, Earl B. Fischer, E. M. Freeman, E. C. Stakman, H. P. Traub, A. C. Arny, W. S. Cooper, Mrs. Pitirim Sorokin, F. K. Butters, C. O. Rosendahl; University of Virginia: Ivey F. Lewis; Wells College: Ida L. Reveley; Wisconsin Academy of Sciences, Arts and Letters: Charles E. Allen, Huron H. Smith, Albert M. Fuller; Yale University: George E. Nichols.

PATRONS

American Ecological Society
American Phytopathological Society
Botanical Society of America
Boyce Thompson Institute for Plant Research
Brooklyn Botanic Garden
Cornell University
The Davey Tree Expert Co.
Gray Herbarium, Harvard University
Missouri Botanical Garden
National Research Council
New York State College of Agriculture
N.Y. Horticultural Society
Philadelphia Society for the Promotion of Agriculture

Rockefeller Institute for Medical Research
Society for Horticultural Science
State Board of Agriculture of Delaware
University of Chicago
University of Delaware
University of Michigan
E. I. du Pont de Nemours and Co.
Niagara Sprayer Co.
New York Insecticide Co.
Pittsburgh Plate Glass Co.
N.V. Potash Export Company
Oakes Ames
A. P. Anderson

N. L. Britton
A. C. Burrage
E. A. Burt
Mrs. W. G. Farlow
Edward Harding
Mrs. Edward Harding
F. D. Kern
Henry Hicks
D. T. MacDougal
Edward Mallinckrodt
L. M. Marble
Barrington Moore
J. B. Overton
B. L. Robinson
J. R. Schramm
Erwin F. Smith
J. G. Townsend, Jr.

SESSIONS OF CONGRESS AS A WHOLE

Three evening sessions of the Congress as a whole were arranged, the first, the formal opening, August 16, being addressed by the President of the Congress, Liberty Hyde Bailey (see Vol. 1, Introduction), and by President Livingston Farrand, who graciously extended the hospitality of Cornell to its guests. At this meeting an invitation from the British Botanists to hold the next International Botanical Congress at London in 1930 was presented by Dr. A. B. Rendle for the committee, composed of himself, Dr. A. W. Hill, and Dr. E. J. Butler (see second paragraph below).

On the occasion of the second and third sessions of the Congress, August 18 and August 20, respectively, invitation addresses were delivered by Prof. F. A. F. C. Went (Vol. 1 pp. 1-12), and by Dr. Erwin F. Smith (Vol. 1 pp. 13-45).

Two business sessions were held August 19 and 20. At the first session a letter of invitation from the British Botanists, as below, was presented for action:—

Linnean Society, Burlington House, London, W. I.

March 10, 1926.

At a representative meeting of British Botanists held in the rooms of the Linnean Society on March 19th, 1926, it was unanimously decided to invite the botanists assembled in Ithaca at the Conference of Plant Sciences in August next, to meet in London in 1930 for the Fifth International Botanical Congress.

Dr. A. W. Hill and Dr. E. J. Butler with the Chairman of the meeting, Dr. A. B. Rendle, were asked to convey the invitation.

A. B. Rendle, Chairman.

After a general expression of interest and anticipation the invitation was, on motion, accepted by acclamation. Following this action a formal vote of thanks was extended to Cornell University and to all those giving time and thought to the work and organization of the Congress. At the second business session all further items of business requiring attention were disposed of. (1) Professor Went reported on the question of the International Union and the steps being taken to promote this organization. He hopes for the adherence of all countries believing that the organization referred to and the International Research Council would tend to extend and perpetuate the common interest of botanists throughout the world. He felt that some division of the organization effected would naturally take over certain duties of the International Association of Botanists. The proposition was discussed but no action was taken, in harmony with the avowed principles of this Congress to enact no legislation in any way committing or tending to regulate the interests of botanists generally. (2) The secretary of the section for Taxonomy, on behalf of the section, presented the following:

"It is the sense of the Fourth International Botanical Congress that the proper maintenance, increase, accessibility and utilization of the great herbaria of the world are matters of international concern not merely to botanical science, but to the nations which benefit through the contributions therefrom to the advancement of civilization."

SPECIAL ACTIVITIES

The limitations of space preclude the presentation of an adequate account of various meetings, both official and unofficial, which provided additional opportunities for contacts both social and scientific, including general entertainments, group meetings and dinners, memorial and complimentary occasions, and sectional or combined excursions. Field trips constituted important aspects of most programs, and in addition to local field trips in the phytogeographically and otherwise interesting environs of Ithaca, longer trips were arranged for the close of the week and later. These included a visit to the Agricultural Experiment Station at Geneva, N.Y., a Niagara Falls excursion, a tour in eastern Canada, and an extended field trip to the Western United States, the latter especially requiring brief mention.

Western Field Trip, August 23 to September 15.—Immediately following the scientific sessions of the Congress a botanical and sight-seeing trip to Yellowstone National Park, Wyo-

ming, was conducted under the leadership of Dr. George D. Fuller, of the University of Chicago, Chicago, Illinois. It occupied about three weeks and provided opportunity for seeing two of the finest national parks in the United States; also other places of historical, botanical and general interest.

Exhibits. Laboratory exhibitions and demonstrations of methods, materials, apparatus, and preparations, representing phases of investigations in process were participated in by about ten of the sections, including about fifty individual exhibits—most of these being referred to in the printed programs distributed at the time. Field exhibits were also arranged by the Cornell representatives of several sections.

Association of Official Seed Analysts of North America. Meetings of this association were held in conjunction with the Congress, with a full program for the four days of regular sessions. The papers presented are not included in these Proceedings. The officers of this Association were as follows:— President: W. H. Wright, Seed Branch, Dept. of Agriculture, Toronto, Canada. Vice-president: Elizabeth F. Hopkins, N. Y. Agricultural Experiment Station, Geneva, N.Y. Secretary-Treasurer: A. L. Stone, University of Wisconsin, Madison, Wisconsin.

SECTIONS OF THE CONGRESS: MINUTES

Section A—Agronomy. *Roy B. Wiggins, Secretary*

The Section held two morning program sessions of invitation papers, exclusively agronomic, and one session in which the Section for Genetics cooperated. On Aug. 20, jointly with the Section for Horticulture, agronomists cooperated with the Section for Physiology. A round table discussion, "The place of statistics in the interpretation of experimental data," led by H. H. Love, continued the program of Tuesday Aug. 17, the Sections for Genetics, Horticulture, and Physiology participating.

Fourteen formal papers were presented by the following: N. M. Tulaikov, O. Arrhenius, H. H. Love, Carlo Cappelletti, D. N. Borodin, T. A. Kiesselbach, L. J. Stadler, A. T. Kirssanoff, H. K. Hayes, C. E. Leighty, J. R. Holbert and J. D. Dickson, N. I. Vavilov (2 papers), D. F. Jones, and D. N. Borodin. These all appear in Volume 1 (pp. 53-173) with the exception of the paper "Dependent segregation" by D. F. Jones, Connecticut Agricultural Experiment Station, for which other publication arrangements were made. Besides the more general botanical excursions, special arrangements were made to visit local experimental field plots, and on Aug. 21 agronomists united with those interested, especially the Sections for Genetics and Horticulture, to inspect the New York Agricultural Experiment Station at Geneva.

Section B—Bacteriology. *James M. Sherman, Secretary*

The morning session of Thursday Aug. 19 was devoted to formal papers concerned with "Morphological and physiological variations in bacteria", Robert S. Breed, Vice-Chairman, presiding. The speakers were: Hilding Bergstrand, Felix Löhnis, Ralph Mellon, and Arthur T. Henrici. On Friday, Aug. 19, papers were presented by Robert E. Buchanan, Selman A. Waksman, B. Issatchenko, and B. Issatchenko and A. Salimowska. The Section for Physiology cooperated in a joint discussion of oxidation and reduction phenomena, with a formal paper by Wm. Mansfield Clark. The papers mentioned appear in Volume 1 (pp. 175-242) with the exception of "The relation of bacterial variability to their life cycles with special reference to a sexual cycle" by Ralph T. Mellon, Highland Hospital, Rochester, N.Y., the major aspects of which had been published in advance. The bacteriologists arranged as a part of their program cooperation with the Sections for Physiology, Pathology, Mycology, and Taxonomy.

The following resolutions relating to nomenclature were adopted by the section:—

That the International Interim Committee, or some other competent committee—

1. Be asked to draft an amendment to the International Botanical Code which will indicate clearly the nomenclatural status and disposition of names of organisms transferred from the animal kingdom to the plant kingdom, such amendment to be presented to the next international botanical congress.

2. Be requested to draft an amendment to the International Botanical Code which will clearly and definitely exclude bacteriological nomenclature from the requirement of a latin diagnosis of new forms described, such amendment to be presented to the next international botanical congress.

3. Be informed that in the opinion of this Section there is no sufficient reason for the establishment of a point of departure for the nomenclature of the bacteria subsequent to 1753, and that this Section suggests that this date be incorporated into the International Botanical Code.

4. Be informed of the suggestion of this section that greater emphasis should be placed in the International Code upon the so-called "type concept," but with the request that no provision be incorporated which will make necessary the designation of a "type or standard specimen", in the ordinary botanical sense, for bacteria.

5. Be requested to select a special international and representative committee of bacteriologists, which committee may have as its particular function the coordination of the particular nomenclatural interests of bacteriologists with those of other botanists, such committee to report its findings and recommendations through the regular channels in preparation for the next international botanical congress.

6. Be requested to prepare for submission to the next international botanical congress an amendment to the International Rules of Botanical Nomenclature which will provide for the appointment of a permanent International Commission on Botanical Nomenclature which shall have duties and responsibilities similar to those of the International Commission in Zoological Nomenclature.

Section C—Cytology. *Lester W. Sharp, Secretary*

The sessions were opened with a brief introductory address by the chairman, George Tischler, University of Kiel, Germany. In his address the chairman stressed some of the peaceful accomplishments of scientific work and the importance of internationalism in science. Five regular sessions of the Section were held, two of these being arranged jointly with the Section for Genetics. Round table discussion periods occupied two afternoons, one conducted jointly with the Section for Genetics on the topic "The cytology of hybrid plants," led by T. H. Goodspeed; in the other period the Section for Cytology cooperated with the section for Physiology in the discussion of "The physical chemistry of protoplasm," led by B. M. Duggar. A joint session with the Sections for Genetics and Taxonomy was arranged as a symposium, "The significance of taxonomic units and their natural basis," the participants in this discussion being mentioned under Taxonomy. At the regular sessions papers were read by B. Nemec, W. Seifriz, Nils Svedelius, W. R. Taylor, M. Levine, Kathleen B. Blackburn, Otto Heilborn, R. A. Harper, R. E. Cleland, C. E. Allen, and Karl Sax (Volume 1, pp. 243-350). In the absence of the authors, abstracts were read by the chairman of papers by M. Nawaschin and T. Sakamura and I. Stow. Members of the Section participated in field excursions and in visits to the experimental plots of various departments of the New York State College of Agriculture.

Section D—Morphology, Histology and Paleobotany. *Duncan S. Johnson, Secretary*

The work of the section was introduced with an address disclosing the broad field of opportunity in research, especially in the borderlands between morphology and the newer divisions of experimental botany, by the chairman, Robert Chodat, University of Geneva, Switzerland. The section held regular scientific sessions on four forenoons, in one of which the Section for Taxonomy cooperated, the topic being "The phylogeny of the angiosperms." Formal papers were presented by F. A. F. C. Went, John T. Bucholz, W. D. Hoyt, Rudolf Florin, J. Hutchinson, Arthur J. Eames, G. R. Wieland, Nils Svedelius, Charles J. Chamberlain, R. B. Thompson, and Robert Chodat. An exhibition of anatomical and paleobotanical materials was held, and suitable excursions were arranged.

SECTION E—ECOLOGY. *H. L. Shantz, Secretary*

In opening the program of sectional meetings Chairman Eduard Rübel, in a short introductory address, outlined the correlation of this Congress with previous congresses and stressed the continuity of purpose in ecological gatherings. In the regular program 19 papers were presented. Of these 16 are printed in Volume 1 (pp. 479-691), by Karel Domin, C. Conzati, Amelio del Villiar, Carl Skottsberg, J. W. Toumey, Alvar Palmgren, G. E. Du Rietz (two papers), H. A. Gleason, G. E. Nichols, W. Szafer, A. Borza, Rutger Sernander, W. H. Pearsall, A. G. Tansley, H. C. Cowles. W. S. Cooper, University of Minnesota, presented a paper, "The fundamentals of vegetational change," for which previous arrangements for printing had been made. Two additional papers were submitted by abstract, those of W. Szafer and W. H. Brown. The section also took part in a joint discussion with the Sections for Horticulture and Physiology on the subject of "Photoperiodism." Special excursions were arranged, and at the close of the Congress several of the ecologists took part in an extended trip, including the Yellowstone National Park.

At a business session the Section appointed the following *ad interim* committee on Phytogeography to form a link between the present Congress and the proposed international botanical congress of 1930, the representatives being as follows: Rübel (Switzerland), Cowles (U. S. A.), Diels (Germany), Du Rietz (Sweden), Pavillard (France), Szafer (Poland), Tansley (Great Britain).

SECTION F—FORESTRY. *Ralph S. Hosmer, Secretary*

In opening the program of the Section on Aug. 17, the chairman, Tor Jonson, Stockholm, Sweden, briefly welcomed the members and emphasized the value of international contacts in forestry. Four morning sessions were held for the presentation of invitation papers, one of these being arranged jointly with the Section of Ecology. The following presented papers on topics pertaining primarily to forestry: Arrigo Serpieri and E. Aldo Pavari, C. D. Howe, J. W. Toumey, Tor Jonson, Raphael Zon, A. Rodger, E. N. Munns, A. J. Cajander, and Sven Petrini. Afternoon sessions included a symposium on "International forest bibliography" and a round-table discussion of "Reorganization of the international Association of Forest Experiment Stations." Other activities of the section included excursions to points of interest and an evening devoted to an exhibition of reels of motion pictures illustrating the work of the Forest Service, U. S. Department of Agriculture.

In business session the Section expressed the need of an International forestry bibliography. Accordingly a resolution prevailed approving the organization of an International Forest Bibliographic Commission and inviting those nations having a forestry organization to establish a National Forestry Commission, the chairman of which shall be a member of the International Forest Bibliographic Commission. Further, resolving, that the International Forest Bibliographic Commission have an executive committee of five members, the duty of which shall be to decide what organization shall issue a bibliography and to devise means for carrying on the work. The desirability of encouraging publication of international forest dictionaries was clearly presented. The round-table discussion of the "Reorganization of the international union of forest experiment stations" led to the formulation of the following:

Resolved that this meeting expresses its gratification with the plan for the reestablishment of the International Union of Forest Experiment Stations, and expresses the hope that it may be reorganized on a permanent and adequate basis.

SECTION G—GENETICS. *Charles E. Allen, Secretary*

The scheduled program of papers was introduced with a short introductory address by the chairman, Professor Ernst Lehmann of the University of Tübingen. The program included both forenoon and afternoon sessions, also one evening meeting. Two of these sessions were arranged jointly with the Section for Cytology, one with the Sections for Cytology and Taxonomy ("The significance of taxonomic units and their natural basis"), and two in which there was cooperation with the Section for Agronomy. The papers more particularly accredited to this section (Volume 1, pp.: 787-946) include those of Ernst Lehmann, M. J.

Sirks, Giulio Savastano, Georg Tischler, A. F. Blakeslee, Edmund Malinowski, G. H. Shull, E. M. East, H. J. Muller, W. H. Eyster, and M. Demerec. A paper read by L. F. Randolph, Cornell University and the U. S. Department of Agriculture, was not presented for publication. The following papers were read by title: "The constructive moments in the origin of forms" by N. P. Krenke of the Timiriasev Federal Institute of scientific research, Moscow, and "Mutations in fungi," F. Chodat of the University of Geneva. In addition to individual participation in shorter excursions, geneticists as a body joined in the more general excursion to the New York Agricultural Experiment Station, Geneva.

Section H—Horticulture. *A. J. Heinecke, Secretary*

Under the chairmanship of Fred J. Chittenden, Royal Horticultural Society, London, three sessions were devoted to papers more exclusively horticultural, one of these, however, having the cooperation of the physiologists. In addition, the Section cooperated in two programs arranged respectively by the Section for Agronomy and the Section for Physiology, and, further, held three round-table discussions. The formal papers (Volume 2, pp. 953-1080) were presented by W. T. Macoun, N. E. Hansen, U. P. Hedrick, Felix Kotowski, F. A. Waugh, G. F. Potter and T. G. Phillips, E. L. Overholser, T. Wallace, Lucien Daniel, H. A. Jones, W. W. Garner, E. C. Auchter, A. L. Schrader, and H. D. Hooker. The topics of the round-table discussions arranged primarily by this section were the following: "Interrelation between photoperiod, temperature, and nutrition and the influence on plant behavior, with especial reference to flowering versus vegetation," "Problems of improvement of varieties, stocks, and methods of propagation," and "Problems of harvesting, handling, and cold storage of flowers, fruits, and vegetables." Among particular phases of the topic last mentioned, the discussion centered around factors in the determination of maturity, bitter pit and scald of apple, the proper storage temperature for various fruits, the effects of temperatures below freezing, and humidity and temperature in the keeping of cut flowers.

Section I—Physiology. *O. F. Curtis, Secretary*

The four forenoon sessions were occupied with the regular program of invitation papers, one period being a joint session arranged by the Section for Horticulture. Papers were presented by A. Ursprung (read by William A. Beck), H. S. Reed, B. E. Livingston, S. Kostytschew (read by abstract), W. W. Lepeschkin, W. J. Robbins, L. Michaelis, J. Stoklasa, George W. Scarth, F. E. Lloyd, N. A. Maximow, T. V. Vouk, M. Popoff, Lewis Knudson, and K. Shibata (see Volume 2, pp. 1081-1193). A paper on "The pigments of photosynthesis" by V. Lubimenko was also read but earlier publication occurred. An exhibition of the activities of the contractile vacuole of *Spirogyra* was presented by F. E. Lloyd as moving pictures, and his paper represents the discussion of this topic. The afternoon sessions consisted of joint sessions with the Sections of Agronomy, Genetics, and Horticulture, Horticulture and Ecology, with the Section for Bacteriology, and the Section for Cytology.

Section J—Pathology. *D. Reddick, Secretary*

The scientific sessions were held under the chairmanship of Dr. E. van Slogteren, Lisse, Holland, and the attendance was often above 150 persons. The program consisted of four morning sessions devoted exclusively to invitation papers, and of afternoon sessions made up of three round-table discussions and one period of "Proposals." In general, the afternoon meetings were utilized for more extended discussion of the topics around which the forenoon papers centered. One entire program was given up to "Biologic considerations of the international movement of plants and plant products." Papers along varied lines were presented by H. Morstatt, H. H. Whetzel, M. Hollrung, H. M. Quanjer and Paul Murphy, C. L. Shear, D. Reddick, B. M. Duggar, H. Klebahn, L. O. Kunkel, Ernst Küster, J. C. Walker, Ruth F. Allen, Marie P. Löhnis, L. R. Jones, F. Beauverie, Z. Zweigbaumowna, H. T. Güssow, E. van Slogteren, E. J. Butler, and a paper of Et. Foex was read by abstract in the absence of the author. Round-table discussions were led by James Johnson and H. B. Humphrey. Demonstrations and exhibits gave opportunity for much informal discussion, and special plant inspection trips were arranged.

The following resolutions were adopted by the Section:

1. That, in mycological nomenclature, particularly in reference to parasitic fungi, we follow the internationally established rules of botanical nomenclature, recognizing in this branch of botany definite *nomina conservanda.*

2. That we endorse the proposal made by D. Reddick, that greater facilities be provided for the production and exchange of disease-resistant varieties of plants; and that the chairman of the Section appoint a committee to devise ways and means of putting the proposal into effect.

3. That we favor the holding of international phytopathological conferences at the same time and place as the meetings of the International Institute of Agriculture are held, with the understanding that we continue to meet also, as heretofore, with the International Botanical Congress.

4. That we urge international cooperation in the study of a biological basis for plant quarantine as a guide to future action, and that the chairman appoint a committee to promote the objects of this resolution.

5. That it is the sense of this Section that there is urgent need among plant pathologists for a more universal recognition of the symptoms of virus diseases of potatoes and of similar diseases of other plants, and need of greater uniformity in the naming of these diseases. We urge, therefore, that more accurate descriptions be made, and especially that they be supported by adequate illustrations. Also, the chairman was authorized to appoint a committee to urge interested countries to send delegates to the proposed International Conference of Phytopathology scheduled to be held in Prague in 1927.

SECTION K—PHARMACOGNOSY and PHARMACEUTICAL BOTANY. *H. W. Youngken, Secretary*

The first session was opened with a paper by the chairman, Henry H. Rusby, Columbia University (see Volume 2, pp. 1356-1360). Invitation papers were continued throughout the four morning sessions, with adequate time for profitable discussion. The following presented or sent papers (Volume 2, pp. 1361-1412): Heinrich Zörnig, W. Brandt, Zdenek F. Klan and Oliver A. Farwell, Henry H. Rusby, R. Wasicky, Charles C. Plitt, T. J. Starker, A. J. Schwarz, George D. Beal, Fanchon Hart, Carl Mez, and C. W. Ballard. Three of the papers constituted a part of a symposium on cascara sagrada. A round-table discussion on "digitalis" was led by Arno Viehoever. Associated with the work of the Section was that of the Plant Science Laboratory Seminar, presided over by E. L. Newcomb. The Section also participated in the round-table discussion of nomenclature, arranged by the Section for Taxonomy, also in scheduled excursions.

SECTION L—TAXONOMY. *K. M. Wiegand, Secretary*

Four regular sessions for the presentation of formal invitation papers were held, the speakers being E. de Wildeman (by proxy), T. A. Sprague, L. H. Bailey, A. S. Hitchcock, John Briquet, H. M. Hall, S. Illichevsky (2 papers), K. M. Wiegand, Arthur W. Hill, M. L. Fernald, C. H. Ostenfeld, LeRoy Abrams, A. B. Rendle, Aven Nelson, P. A. Rydberg, and Carl Skottsberg. The papers presented appear in Volume 2. "Botanical nomenclature" was the subject of a round-table discussion participated in especially through papers by John Briquet, Marshall A. Howe, M. L. Fernald, and N. L. Britton (Volume 2, pp. 1556-1570).

A joint symposium was arranged with the cooperation of the Sections for Cytology and Genetics. Subject: "The significance of taxonomic units and their natural basis. Various viewpoints were presented by H. M. Hall, Otto Heilborn, G. H. Shull, and N. F. Vavilov, with discussions by K. M. Wiegand, W. R. Taylor, B. M. Davis, and R. A. Harper (Volume 2, pp. 1571-1589). The section also included in its program a symposium on botanical nomenclature arranged by the Section for Mycology; likewise cooperated with the section for Morphology and Paleobotany in a symposium on the "Phylogeny of Angiosperms." Special excursions and informal meetings for discussion were arranged. The following papers, in the absence of the authors, were read by title: "Taxonomy in relation to various evolutionary theories," S. Schonland, Rhodes University College, Grahamstown, Cape Colony, South Africa. "Note on nomenclature," G. C. Druce, Oxford University, Oxford, England; "Beiträge zur Nomenclature

der ostasiatischen Mertensia Arten," A. Brand, Sorau, Germany; "Revision du genus Mazus. Le genre Alectra Thunb. à Madagascar. Decarynthus, a new genus of Scrophulariaceae," G. Bonati, Lure, France.

Resolutions adopted by the Imperial Botanical Congress, London, 1924 (see Report of Proceedings, pp. 301-307), and by the Committee on Australian Botanical Nomenclature, 1925, and a list prepared by Miss M. L. Green to exemplify the standard species idea were presented on behalf of the Imperial Congress and of the Australian·Committee by T. A. Sprague.

Resolutions from the Botanical Society of America were presented by A. S. Hitchcock. These related to the appointment of an International Interim Committee and to the modification of the International Rules.

Discussion on these resolutions was deferred. On motion it was voted that a temporary committee of five be appointed by the chairman to nominate a standing *ad interim* committee to consider the subject of plant nomenclature and to make such recommendations as might seem desirable to the next botanical congress, at London in 1930. It was stipulated that one member of the committee should be the chairman of the round-table, two others should be John Briquet and A. B. Rendle, and that the remaining two members should have special knowledge of cryptogams. The chairman appointed A. S. Hitchcock, John Briquet (chairman), A. B. Rendle, J. C. Arthur, and C. H. Ostenfeld.

This nominating committee later reported the names of the following persons to constitute the *ad interim* committee, and on vote of the section assembled in round-table these persons nominated were elected: J. H. Barnhart (U.S.A.), G. Bitter (Germany), Black (Australia), J. Briquet (Switzerland), A. von Degen (Hungary), E. de Wildeman (Belgium), E. Diels (Germany), K. Domin (Czechoslovakia), B. Fedtschenko (U.S.S.R.), H. Harms (Germany), A. S. Hitchcock (U.S.A.), A. de Jaczewski (U.S.S.R.), E. Janchen (Austria), H. Lecomte (France), H. Lindberg (Norway), E. Maire (Algiers), L. A. Mangin (France), C. E. Moss (South Africa), S. Murbeck (Sweden), T. Nakai (Japan), C. H. Ostenfeld (Denmark), J. Ramsbottom (England), A. B. Rendle (England), B. L. Robinson (U.S.A.), H. Schinz (Switzerland), C. L. Shear (U.S.A.), T. A. Sprague (England), A. Trotter (Italy), T. Valeton (Holland).

This action of the section was reported to the Congress in general business session and was approved by the Congress.

It was moved by A. B. Rendle that John Briquet and H. Harms occupy positions on this committee similar to those occupied by them on the Permanent Nomenclature Commission of the Brussels Congress, namely, John Briquet chairman, and H. Harms vice-chairman. The motion was unanimously carried.

It was voted to take no action on the resolutions prepared at the Ithaca Congress but to refer them to the above committee. Similar disposal was made of the resolutions on nomenclature prepared by the Section for Bacteriology (see p. 1777) and presented by R. S. Breed.

Section M—Mycology. *H. M. Fitzpatrick, Secretary*

Four sessions of the invitation program were arranged for the forenoons of those days devoted to this purpose, the first program being opened with a paper by the chairman, E. J. Butler, followed by E. A. Burt and C. A. Kauffman. The remaining programs consisted of papers by H. W. Wollenweber, C. L. Shear, A. H. R. Buller, W. B. Brierley, K. Wize, E. M. Wakefield, J. Ramsbottom, L. O. Overholts, G. H. Cunningham, J. C. Arthur, H. Klebahn, J. H. Faull, and Carlton Rea. An afternoon symposium on nomenclature included discussion papers by C. L. Shear, J. Ramsbottom, J. C. Arthur, and C. H. Kauffman, while a second symposium gave consideration to the topic "Evolutionary and cytological problems in rusts," with papers submitted by H. S. Jackson, J. Ramsbottom, B. O. Dodge, E. B. Mains, and E. C. Stakman. Papers received by the secretary, authors not in attendance, were those of P. Dietel, Zwickau, Germany, "Betrachtungen über die geographische Verbreitung der Uredineen," and of W. Siemaszko, College of Agriculture, Skierniewice, Poland, "Studies of the Polyporaceae in Poland." Other papers announced but not presented were read by title. Special excursions were arranged.

ATTENDANCE[1]

Aaron, Isador M. Pennsylvania State College

Abrams, LeRoy. Stanford University

Ackley, Alma B. Detroit City College

Adams, James F. University of Delaware

Addoms, Ruth M. University of Wisconsin

Adriano, Felipe T. Los Banôs College, Philippines

Agati, Julian A. University of the Philippines

Allen, Charles E. University of Wisconsin

Allen, Ruth F. U. S. Dept. Agriculture (Berkeley)

Altenburg, Rachel. Western State Normal School (Michigan)

Altenburg, Virgil. Western State Normal School (Michigan)

Andersen, Alice M. U. S. Dept. Agriculture

Anderson, Emma N. University of Nebraska

Anderson, Gladys P. Rahway, New Jersey

Andes, J. O. Tennessee Agric. Exp. Station

Andrews, F. M. University of Indiana

Anthony, R. D. Pennsylvania State College

Appel, Otto. Biologische Reichs-Anstalt f. Land- u. Forstwirtschaft, Berlin-Dahlem

Appleman, C. O. University of Maryland

Armstrong, George M. Clemson College

Arnold, Chester A. Cornell University

Arthur, J. C. Purdue University

Artschwager, Ernst. U. S. Dept. Agriculture

Arzberger, E. G. U. S. Dept. Agriculture

Aslander, A. Bolenas, Sweden

Atwood, Alice C. U. S. Dept. Agriculture

Atwood, W. M. Oregon State College

Bach, Walter J. U. S. Dept. Agriculture

Bache-Wiig, Sara. Smith College

Bacigalupi, Rimo. Mills College

Bailey, D. L. Dom. Rust Research Laboratory, Winnipeg

Bailey, Ethel. Ithaca, New York

Bailey, Irving W. Bussey Institution, Harvard University

Bailey, L. H. Ithaca, New York

Bailey, J. S. Mass. Agric. College

Baker, H. R. University of Delaware

Baldwin, Henry I. Brown Company, Berlin, N.H.

Ballard, C. W. Columbia University College of Pharmacy

Banfield, Wm. University of Wisconsin

Barclay, Margaret E. Thomas Jefferson High School, New York City

Barker, Henry D. Port au Prince, Haiti

Barnhart, John Hendley. The N. Y. Botanical Garden

Baron, Arnold. Western State Normal School (Michigan)

Barrus, M. F. Cornell University

Barss, Howard P. Oregon State College

Beach, W. S. Penn. State College

Beattie, R. Kent. U. S. Dept. Agriculture

Beaumont, A. B. Mass. Agric. College

Bechtel, A. R. Wabash College

Beck, Mabell M. Edgewater, N.J.

Beck, William A. University of Dayton

Beckwith, Angie M. U. S. Dept. Agriculture

Beeman, Rebecca A. Smith College

Belden, G. W. Cornell University

Bell, A. F. Queensland University, Brisbane

Beeskow, H. C. University of Chicago

Benedict, H. M. University of Cincinnati

Benham, Rohda W. Barnard College

Bennett, F. P. University of California

Bentley, John, Jr. Cornell University

Bentley, Mrs. John, Jr. Ithaca, New York

Berg, Anthony. University of W.Va.

Berger, Alvin. N. Y. State Agric. Exp. Station

Bergman, H. F. University of Hawaii, Honolulu

Bergstrand, Hilding. Sabbatsberg Hospital, Stockholm

Berkeley, G. H. St. Catharines, Ontario

Bernstein, Mrs. I. S. Brooklyn, N.Y.

Berry, L. T. Va. State Dept. of Agriculture

Bessey, E. A. Mich. State College

Bisby, G. H. Manitoba Agricultural College, Winnipeg

Black, Caroline A. Conn. College

Blackburn, Kathleen B. Armstrong College, Newcastle-on-Tyne

[1] Does not include those registering as visitors, the latter numbering about two hundred and fifty.

Blake, Sidney F. U. S. Dept. Agriculture

Blakeslee, A. F. Carnegie Institution of Washington (Cold Spring Harbor)

Blodgett, F. M. Cornell University

Bodger, Elizabeth M. Cornell University

Boeshore, Irwin. University of Pennsylvania

Borodin, D. N. Russian Agricultural Agency, New York City

Boron, Frances. Western State Normal School (Michigan)

Borza, Alexandre. University of Cluj, Roumania

Bowers, C. G. N. Y. Botanical Garden

Bowman, Paul W. George Washington University

Boyce, Sadie. N. J. Agric. Exp. Station

Boyd, O. C. Ga. State Board of Entomology

Bradley, J. Chester. Cornell University

Bratley, C. O. Cornell University

Bray, William L. Syracuse University

Breed, Robert S. N. Y. Agric. Exp. Station

Breenfield, Mary E. N. J. State Woman's College

Brieger, Frederick G. Bussey Institution, Harvard University

Briquet, John. Conservatoire botanique, Geneva

Broadhurst, Jean. Teachers College, Columbia University

Broadhurst, Winfield. Columbia University

Brooks, Charles. U. S. Dept. Agriculture

Brooks, Matilda M. University of California

Brooks, S. C. University of California

Brown, E.   .

Brown, Harry Philip. N. Y. State College of Forestry

Brown, Helen J. Ohio State University

Brown, William H. Bureau of Science, Manila

Browning, Harold W. R. I. State College

Bryan, Mary K. U. S. Dept. Agriculture

Buchanan, R. E. Iowa State College

Buchholz, John T. University of Texas

Bucholtz, Alexander F. Cornell University

Buckman, H. O. Cornell University

Budington, Robert A. Oberlin College

Buller, A. H. R. University of Manitoba

Bunton, G. W. Ottawa Technical School

Burger, O. F. University of Florida

Burgiss, J. L. N. C. State Department of Agriculture

Burkholder, Paul R. Cornell University

Burkholder, Walter H. Cornell University

Burnham, Stewart H. Cornell University

Burns, G. P. University of Vermont

Burrel, Arthur B. Cornell University

Burt, E. A. Missouri Botanical Garden

Bushnell, John. Agric. Exp. Station, Wooster

Butler, E. J. Imperial Bureau of Mycology, Kew, England

Callister, G. J. Potash Syndicate, New York City

Campagna, Elzear. Ecole d' Agriculture, Quebec

Campbell, William. Western State Normal School (Michigan)

Canis, O. P. M. N. J. College of Pharmacy

Cardoso, Paul W. Cornell University

Carey, Cornelia L. Barnard College, Columbia University

Carlson, Margery C. Boyce Thompson Institute for Plant Research

Carrick, D. B. Cornell University

Carson, A. A. University of Nanking, China

Cash, Edith K. U. S. Dept. Agriculture

Chadwick, L. E. Cornell University

Chamberlain, Charles J. University of Chicago

Chang, C. Y. University of Chicago

Chase, Ethel W. B. College of the City of Detroit

Chen, C. C. Tsing Hua College, Peking

Chittenden, Fred J. Roy. Hort. Soc., London

Chivers, A. H. Dartmouth College

Choate, Helen A. Smith College

Chodat, Robert. University of Geneva, Switzerland

Christoff, Michael. Bussey Institution, Harvard University

Chrysler, M. A. Rutgers University

Clapp, Grace L. Milwaukee-Downer College

Clark, Anna W. Binghampton, New York

Clark, Daniel G. Cornell University

Clark, Wm. M. U. S. Hygienic Laboratory

Clark, Orton L. Mass. Agric. College

Clarke, Elizabeth L. East Corinth, Vt.

Clayton, E. E. N. Y. Agric. Exp. Station, Riverhead

Cleland, Ralph E. Goucher College

Clinton, G. P. Conn. Agric. Exp. Station, Yale University

Clippinger, Florence E. Roosevelt High School, Dayton, Ohio

Clum, Harold H. Syracuse University

Cobb, Stanley J. Penn. State College

Codding, Geo. C. Mount Vernon, New York

Colcard, Mabel. U. S. Dept. Agriculture

Coleman, L. C. University of Toronto

Collison, R. C. N. Y. Agric. Exp. Station

Comte, Ferdinand. Yverdon, Switzerland
Comte, Frederic. Yverdon, Switzerland
Conant, George H. University of Wisconsin
Conn, H. J. N. Y. Agric. Exp. Station
Cook, Harold. Cornell University
Cooley, Jacquelin S. U. S. Dept. Agriculture
Cooper, George Olds. University of Wisconsin
Cooper, H. P. Cornell University
Copeland, Herbert F. Sacramento High School, Calif.
Corbett, Lee C. U. S. Dept. Agriculture
Coulson, John G. Macdonald College, Quebec
Coulter, John M. Boyce Thompson Institute for Plant Research
Cowles, Elizabeth H. University of Chicago
Cowles, Henry C. University of Chicago
Cowles, Henry T. University of Porto Rico
Craig, Edna. Newburgh Free Academy, Newburgh, New York
Crane, M. B. John Innes Horticultural Institution, Merton, London
Crider, F. J. Boyce Thomson Southwestern Arboretum
Crocker, William. Boyce Thompson Institute for Plant Research
Cromer, C. O. Penn. State College
Cullinan, F. P. Purdue University
Currence, Trey M. Cornell University
Curtis, Otis F. Cornell University
Curtis, Ralph Wright. Cornell University

Dahlstrom, Tage G. Svenska Skogsvardsforeningen, Eagersta, Sweden
Dana, S. T. Northwestern Forest Exp. Station, Amherst, Mass.
Dane, Rebecca H. University of Buffalo
Darbker, L. K. University of Pittsburgh
Darlington, Henry T. Mich. State College
Darrow, George M. U. S. Dept. Agriculture
Davenport, Chas. B. Carnegie Institution of Washington, Cold Spring Harbor
Davidson, John. University of British Columbia, Vancouver
Davis, Bradley Moore. University of Michigan
Davis, Emma. Cornell University
Deam, Chas. C. Bluffton, Indiana
Defrance, Jesse A. Colo. Agric. College
Demerec, M. Carnegie Institution of Washington, Cold Spring Harbor
Demeter, Karl J. Hochschule für Landwirtschaft und Brauerei, Weihenstephan bei Muenchen
Deuber, Carl G. Yale University

Dewell, Jr. Burdette G. Albany College of Pharmacy
Diehl, William W. U. S. Dept. Agriculture
Dillon, J. J. Auburn, New York
Dobroscky, Irene D. Boyce Thompson Institute for Plant Research
Dodge, B. O. U. S. Dept. Agriculture
Dodge, Carroll W. Harvard University
Domin, Karel. Charles University, Prague
Dorr, Eleanor M. Cornell University
Dorsey, M. J. University of Illinois
Douglas, G. E. Cornell University
Drachman, Julian M. Columbia University
Duggar, B. M. University of Wisconsin
Dunham, Carrie Allen. Cornell University
Durham, G. B. Conn. Agric. College
DuRietz, G. Einar. Plant Biological Institution, Upsala, Sweden
DuRietz, Greta. Plant Biological Institution, Upsala, Sweden
Dye, H. W. Middleport, New York

Eames, Arthur J. Cornell University
Earl, R. O. Queen's University, Kingston, Ontario
East, E. M. Harvard University
Eastman, M. Gale. University of New Hampshire
Eaton, Frederick S. Conn. College of Pharmacy, New Haven
Eckerson, Sophia H. Boyce Thompson Institute for Plant Research, New York
Edgerton, C. W. Louisiana State University
Edson, H. A. U. S. Dept. Agriculture
Egerton, John B. Calvert Hall College, Baltimore
Egner, Hans. Centralanstalten, Experimentalfeltet, Sweden
Ehlers, John H. University of Michigan
Einset, Olav. N. Y. Agric. Exp. Station
Elliot, George A. Dept. Agriculture, Ottawa
Ellis, Hazel R. Keuka College, Syracuse
Ellis, Zenas H. Fair Haven, Vt.
Emerson, R. A. Cornell University
Engelmann, Mac. Wilmington, Dela.
Ennis, Beulah. Wellesley College
Erlanson, Eileen W. University of Michigan
Evans, Clytee R. Mississippi State College for Women
Eyster, Lewis A. Ithaca, New York
Eyster, William H. Bucknell University

Fagundes, Alvaro B. Pelotas, Brazil
Faull, J. H. University of Toronto

Fawcett, Edna H. U. S. Dept. Agriculture

Fawcett, Howard S. University of California (Riverside)

Felix, E. L. Cornell University

Fenner, L. M. Clemson College

Fergus, E. N. University of Kentucky

Ferguson, John A. Penn. State College

Ferguson, Margaret C. Wellesley College

Ferguson, Opal. Hastings, New York

Fernald, Evelyn I. Conn. College, New London

Fernald, M. L. Gray Herbarium, Harvard University

Fernow, Karl H. Cornell University

Fischer, Earl B. University of Minnesota

Fisk, Emma L. University of Wisconsin

Fiske, J. G. N. J. Agric. Exp. Station

Fitzpatrick, H. M. Cornell University

Florin, Rudolf. Swedish Museum of Natural History, Stockholm

Flynn, John E. Cornell University

Fogelman, Raymond. Paterson, N.J.

Fogg, John M. Jr. University of Pennsylvania

Folsom, Donald. Me. Agric. Exp. Station

Forbes, Reginald D. Southern Forest Exp. Station, New Orleans

Forbes, William T. M. Cornell University

Fortun, Gonzalo M. Santiago de las Vegas, Cuba

Foster, A. S. Bussey Institution, Harvard University

Foster, Anna L. Boston Public Schools

Foulds, Frank. Dept. Agriculture, Winnipeg

Fowler, Mary Lois. Western State Normal School (Michigan)

Fraser, A. C. Cornell University

Fraser, Samuel. Geneseo, N.Y.

Fred, E. B. University of Wisconsin

Freeland, Lester M. Cornell University

French, G. T. Va. State Dept. Agriculture, Richmond

Fromme, F. D. Va. Polytechnic Institute

Fudge, Bonnie Reid. Rutgers University

Fukushi, Teikichi. Hottori Agric. College, Japan

Fuller, Albert M. Public Museum, Milwaukee

Fuller, Geo. D. University of Chicago

Fulton, H. R. U. S. Dept. Agriculture

Gage, Geo. R. De Pauw University

Gager, Stuart C. Brooklyn Botanic Garden

Galleber, Ethel. Western State Normal School (Michigan)

Ganzel, Mrs. Elizabeth. Western State Normal School (Michigan)

Garber, R. J. W.Va. University

Garvey, P. I. Kan. Agric. College

Gathercoal, E. N. University of Illinois (Chicago)

Gates, Frank C. Kan. Agric. College

Genung, Elizabeth F. Smith College

George, Harriet. University of Chicago

Gerry, Eloise. Forest Products Laboratory

Gilbert, B. E. R. I. Agric. Exp. Station

Gilbert, W. W. U. S. Dept. Agriculture

Gillis, M. C. University of Illinois

Gladwin, F. E. N. Y. Agric. Exp. Station

Gleason, H. A. N. Y. Botanical Garden

Glidden, B. J. University of New Hampshire

Gloyer, W. N. Y. Agric. Exp. Station

Godkin, J. V. Va. Polytechnic Institute

Goldstein, Bessie. Columbia University

Gonzalez, L. A. Baliuag, Bulacan, Philippine Islands

Gooding, Alice A. Albany, N.Y.

Gooding, J. H. Wilmington, Del.

Goodlatte, A. B. Columbia University

Goodspeed, T. H. University of California

Gordon, Alexander. Los Banôs, Philippine Islands

Gordon, Anne T. Cornell University

Gortner, Ross Aiken. University of Minnesota

Goss, R. W. University of Nebraska

Gould, H. P. U. S. Dept. Agriculture

Grace, Charles M. Austin High School, Chicago

Graham, Margaret A. Hunter College, New York City

Grattan, George E. Seed Branch, Dept. Agriculture, Ottawa

Graves, Arthur H. Brooklyn Botanic Garden

Greenman, J. W. Missouri Botanical Garden

Gress, E. M. Penn. Dept. Agriculture, Harrisburg

Griffin, E. L. University of California

Griffiths, Marion A. U. S. Dept. Agriculture

Griswold, Sylvia M. Penn. College for Women, Pittsburgh

Gugan, Jean M. Dom. Dept. Agriculture, Ottawa

Gundersen, Alfred. Brooklyn Botanic Garden

Gunther, Edmund. Ann Arbor, Michigan

Güssow, H. T. Experimental Farm, Ottawa

Gustafson, Felix A. University of Michigan

Guterman, Carl E. F. Cornell University

Haan, Raymond H. Western State Normal School (Michigan)

Haas, A. R. C. University of California (Riverside)

Haber, Mrs. Vernon R. Penn. State College

Haenseler, C. M. N. J. Agric. Exp. Station

Hagan, William A. Cornell University

Halushka, Meyer. John Marshall High School, Chicago

Haines, George. U. S. Dept. Agriculture

Haley, D. E. Penn. State College

Hall, H. M. Carnegie Institution of Washington, Berkeley, Calif.

Hammond, Roydon L. Del. State Board of Agriculture, Dover

Hansen, N. E. S. D. State College of Agriculture

Hardenburg, E. V. Cornell University

Harding, Edward, Mrs. Plainfield, New Jersey

Harlan, J. D. N. Y. Agric. Exp. Station

Harper, R. A. Columbia University

Harper, R. A. Mrs. Ridgewood, New Jersey

Harrington, Geo. T. New York City High Schools

Harris, Henry C. Cornell University

Hart, F. Columbia University College of Pharmacy

Hart, Constance E. St. Lawrence University

Hartzell, Albert. Boyce Thompson Institute for Plant Research

Hartshorn, R. H. Cornell University

Hartwell, B. L. R. I. Agric. Exp. Station

Hartzell, Frederick Z. N. Y. Agric. Exp. Station

Haskell, R. V. U. S. Dept. Agriculture

Hayes, H. K. University of Minnesota

Hazen, Tracy E. Barnard College, Columbia University

Hedges, Florence, U. S. Dept. Agriculture·

Hedrick, U. P. N. Y. Agric. Exp. Station

Heilborn, Otto. Stockholms Hogskola, Sweden

Heimlich, L. F. Valparaiso University

Hein, Illo. Columbia University

Heinicke, Arthur John. Cornell University

Henderson, Lena B. Rockford College

Henrici, Arthur T. University of Minnesota

Hesler, L. R. University of Tennessee

Hicks, Henry. Westbury, New York

Higgins, B. B. Ga. Agric. Exp. Station

Hildreth, A. C. University of Minnesota

Hill, J. B. Penn. State College

Hill, A. W. Royal Botanic Garden, Kew

Hinds, Annette E. Russell Sage College

Hires, Clara S. Cornell University

Hitchcock, A. S. U. S. Dept. of Agriculture

Hoffer, George N. Purdue University

Hollick, Arthur. N. Y. Botanical Garden

Holbert, J. R. U. S. Dept. Agriculture

Hollrung, Max. University of Halle, Germany

Holmes, Albert. Western State Normal School (Michigan)

Holmes, F. S. University of Maryland

Holmes, Frances O. Boyce Thompson Institute for Plant Research

Holroyd, Roland. University of Pennsylvania

Honey, Edwin E. Washington State College

Hooker, Henry D. University of Missouri

Hopkins, Elizabeth F. N. Y. Agric. Exp. Station

Hopkins, E. F. Cornell University

Horsfall, James G. Cornell University

Horton, Ethel Sue. University of Minnesota

Hosmer, Ralph S. Cornell University

Hosmer, Mrs. R. S. Ithaca, New York

Houghton, Clinton O. University of Delaware

Howard, Frank L. Cornell University

Howe, Clifton D. University of Toronto

Howe, Marshall A. N. Y. Botanical Garden

Howe, Thomas D. James Millikin University

Howitt, John Eaton. Ontario Agricultural College

Howlett, Freeman S. Ohio Agric. Exp. Station

Hoyt, W. D. Washington and Lee University

Humphrey, Harry B. U. S. Dept. Agriculture

Humphrey, S. S. Ohio State University

Hunt, W. R. Conn. Agric. Exp. Station

Hunter, Mabel R. High School, Cleveland, Ohio

Hursh, Charles R. Boyce Thompson Institute for Plant Research

Hutchins, L. M. U. S. Dept. Agriculture

Ida, Goro. Imperial University, Tokyo

Ishikawa, M. Imperial University, Tokyo

Issatchenko, B. Botanical Gardens, Leningrad

Jackson, Gemma. Cornell University

Jackson, H. S. Purdue University

Jackson, Marie. N. Y. Agric. Exp. Station

Jehle, R. A. University of Maryland

Jenkins, Anna E. U. S. Dept. Agriculture

Jenkins, Bernice. Boyce Thompson Institute for Plant Research

Jenings, O. E. Carnegie Museum and University of Pittsburgh

Jennings, Mrs. O. E. Pittsburgh

Jennison, H. M. University of Tennessee

Jepson, W. L. University of California

Joffe, Jacob S. Rutgers University

Johansson, Folke. Forest Service, Stockholm

Johnson, A. G. U. S. Dept. Agriculture

Johnson, Duncan S. Johns Hopkins University

Johnson, Edward M. University of Kentucky

Johnson, Frank W. Buffalo Society Natural Sciences

Johnson, James. University of Wisconsin

Johnston, Ivan M. Gray Herbarium, Harvard University

Johnston, John R. United Fruit Company, Boston

Johnstone, George R. University of Southern California

Jones, D. F. Conn. Agric. Exp. Station

Jones, Henry A. University of California

Jones, Leon K. N. Y. Agric. Exp. Station

Jones, L. R. University of Wisconsin

Jonson, Tor. College of Forestry, Stockholm

Jud, Frieda C. New York City

Jurica, Hilary S. St. Procopius College, Lisle, Illinois

Kanouse, Bessie B. University of Michigan

Karrer, Annie May Hurd. U. S. Dept. Agriculture

Kasparian, H. M. Cornell University

Kaufmann, B. P. University of Pennsylvania

Kauffman, C. H. University of Michigan

Keitt, G. W. University of Wisconsin

Keileter, Paul D. N. Y. State College of Forestry, Syracuse

Kelley, Arthur P. Rutgers University

Kelly, James P. Penn. State College

Kelly, Margaret Patricia. U. S. Dept. Agriculture

Kenoyer, Leslie A. Western State Normal School (Michigan)

Kern, Frank Dunn. Penn. State College

Kibbe, Alice L. Carthage College, Ill.

Kier, Leone. Western State Normal School (Michigan)

Kiesselbach, T. A. University of Nebraska

Knightlinger, Clifford V. Cornell University

Kinsella, Jane C. Purdue University

Kirby, R. S. Penn. State College

Kirssanoff, Alexander. Institute of Experimental Agronomy, Leningrad

Kivikoski, B. R. Legation of Finland, Washington

Klebahn, Henrick. University of Hamburg, Germany

Klebahn, Ludwig. Hamburg, Germany

Knappen, Mrs. N. C. George Washington University

Knappen, Phoebe. Cornell University

Knight, Howard L. U. S. Dept. Agriculture

Knott, James E. Penn. State College

Knowlton, H. E. West Virginia University

Knudson, Lewis. Cornell University

Koch, Minna F. Cornell University

Koffel, Wm. Lehr. Western State Normal College (Michigan)

Kohl, E. J. Purdue University

Korstian, C. F. Appalachian Forest Exp. Station, Asheville, N.C.

Kotowski, F. College of Agriculture, Warsaw, Poland

Kouma, Takuji. Kyushu Imperial University, Japan

Krenz, Mathilde H. University of Illinois

Krieger, Gertrude. Western State Normal College (Michigan)

Krishna, P. G. Picket Secumderrabad (Dn) India

Kunkel, L. O. Boyce Thompson Institute for Plant Research

Küster, Paul. Botanischer Garten, Breslau

LaGarde, V. L. Missouri Botanical Garden

Laissuer, G. N. Plant Breeding Institute, Svalof, Sweden

Larson, Alvin H. University of Minnesota

Larsen, Orpha. Western State Normal College (Michigan)

LaRue, Carl D. University of Michigan

Laubengayer, R. A. Cornell University

Lavis, Charles A. Mich. State College

Lebedef, Dr. University Rostov-Don, U.S.S.R.

Lee, H. Atherton. Exp. Station, Hawaiian Sugar Planters' Association, Honolulu

Leggatt, C. W. Dept. Agriculture, Calgary, Alberta

Lehmann, Ernst. Botanisches Institut, Tübingen

Leighty, Clyde E. U. S. Dept. Agriculture

Leonian, Leon H. University of West Virginia

Levine, Michael. Montefiore Hospital, New York City

Lewcock, H. K. University of Adelaide, Australia

Lewis, June E. Western State Normal College (Michigan)

Lewis, R. Donald. Cornell University

Lewis, Sara. Northwestern University

Libby, Mrs. Harriet M. Ithaca, New York

Lindahl, Karl F. Svenska Skogsvardsfore, Brundkog, Sweden

Lindstrom, E. W. Iowa State College

Linford, Maurice B. University of Wisconsin

Link, George K. University of Chicago

Lipman, Jacob. Rutgers University

Livingston, Burton E. Johns Hopkins University

Lloyd, F. E. McGill University

Lodewick, Elton J. N. Y. State College of Forestry, Syracuse

Löhnis, Marie P. Scheveningen, Holland

Loomis, W. E. University of Arkansas

Love, H. H. Cornell University

Lubimenko, Valdimir N. Botanical Gardens, Leningrad

Lute, Anna M. Colo. Agric. College

MacArthur, John W. Ontario Agricultural College

MacDaniels, L. H. Cornell University

MacLeod, Donald J. Dept. Agric, Ottawa

MacMillan, W. B. Penn. State College

Macoun, W. T. Central Exp. Farm, Ottawa

Magee, Charles J. Dept. Agriculture, New South Wales

Maines, E. B. Purdue University

Maiwald, Kurt F. G. University of Breslau, Germany

Malinowski, E. College of Agriculture, Warsaw, Poland

Malte, M. O. National Herbarium of Canada, Ottawa

Mangelsdorf, P. C. Conn. Agric. Exp. Station

Mann, Mary Lee, Columbia University

Manning, Wayne E. Cornell University

Manns, Thomas F. University of Delaware

Marcello, A. San Fautin, Venice, Italy

Markle, M. S. Earlham College

Marsh, R. S. University of Illinois

Marshall, Rush P. U. S. Dept. Agriculture

Martin, G. Hamilton, II. U. S. Dept. Agriculture

Martin, Thomas L. Brigham Young University

Martin, Wm. H. Rutgers University

Martinovitch, Peter N. Syracuse University

Mason, Carol Y. University of Illinois

Massey, L. M. Cornell University

Matheson, Robert. Cornell University

Matsuda, Hideo. Imperial University, Tokyo

Matthews, Donald M. Tropical Plant Research Foundation, Washington

Maximow, Nicolas A. Institute of Applied Botany and New Cultures, Leningrad

Maximow, Mrs. T. Institut of Applied Botany and New Cultures, Leningrad

May, Curtis. Ohio Agric. Exp. Station

McAllister, Ellen C. Ithaca, New York

McCallan, S. E. A. Cornell University

McClintock, Barbara. Cornell University

McClintock, J. A. University of Tennessee

McConkey, O. Ontario Agricultural College

McCool, M. M. Mich. State College

McCormick, Florence A. Conn. Agric. Exp. Station

McCrea, Adelia. Parke, Davis and Company, Detroit

McCreary, Otto. Cornell University

McCubbin, W. A. Penn. Dept. Agriculture, Harrisburg

McCullough, Charlotte S. Seed Branch, Dept. Agriculture, Ottawa

McCulloch, Myrtle A. Dept. Agriculture, Ottawa

McCullock, Lucia. U. S. Dept. Agriculture

McElreath, Marie. University of Chicago

McLean, Fonnant. R. I. Agric. Exp. Station

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